

NOTES ON NORTH AMERICAN SPECIES OF *POLYDRUSUS* GERMAR

(COLEOPTERA: CURCULIONIDAE, BRACHYDERINAE)

17. A contribution to the knowledge of the Curculionoidea.

ELBERT L. SLEEPER

Department of Zoology and Entomology, The Ohio State University, Columbus 10

The genus *Polydrusus* includes about 188 species, most of which are native to the palearctic region. The *Coleopterorum Catalogus* records only 21 species from the western hemisphere—11 from Mexico and Central America; 2 from South America; 2 from the West Indies (Guadeloupe); and 6 from North America (1 from lower California, 2 introduced European species, and 3 native to the United States).

In 1909, Pierce transferred the Lower Californian *Scythropus delicatulus* Horn to *Polydrusus*. This transfer is not recorded in the *Catalogus* but is noted in Blackwelder's 1947 list of Neotropical Coleoptera.

In 1950, Kuschel reviewed the Chilean forms, naming three new species. In listing the synonymies of Neotropical Curculionidae in 1955, he transferred *Phyllobius roseus* Blanchard to *Polydrusus*, thereby reducing his species *robigo* to a synonym of the former. He also removed *morosus* Boheman from *Polydrusus* to *Anisactus* Kuschel and *P. vagabundus* Boheman to *Heteractis* Kuschel of the Anyopactini.

These taxonomic changes bring the number of species recorded from the western hemisphere to 23 — 11 from Mexico and Central America; 3 from South America; 2 from the West Indies; and 7 from North America, 2 of the latter from lower California. To this list I am adding a new species from Arizona, bringing the total number of *Polydrusus* known from the western hemisphere to 24.

The species treated in this paper are as follows:

Native American Species

americanus Gyllenhal, 1834, p. 136; type locality, America borealis.

dorsalis Horn, 1876, p. 105; type locality, Missouri. Specimens of *americanus* have been compared with the type of *dorsalis* in the Museum of Comparative Zoology and this synonymy confirmed.

decoratus Woodruff, 1923, p. 155; type locality, Hazen, Alabama.

delicatulus (Horn), 1894, p. 444, (*Scythropus delicatulus*); type locality, El Taste, Lower California. *Polydrusus delicatulus* (Horn), Pierce, 1909, p. 363.

hassayampus, new species; type locality, Constellation, Arizona.

ochreus Fall, 1907, p. 264; type locality, Cloudercroft, New Mexico.

peninsularis Horn, 1894, p. 445; described from Coral de Piedre, El Taste, and San Jose del Cabo, Lower California.

Introduced European Species

impressifrons Gyllenhal, 1834, p. 140; described from Gallia and Germania. For references in the American Literature see Index of American Economic Entomology, vols 1, 2, 5 and 9.

sericeus (Schaller), 1783, p. 286, (*Curculio sericeus*); described from Europe. For American records see Britton, 1934, p. 474; Frost, 1946, p. 51.

Key to the North American Species of *Polydrusus* Germar

1. Mandibles with 3 or less setae each, no other vestiture present; scape not surpassing eye; dorsal scales green. 2
- 1'. Number of setae or setae and small scales, on each mandible, 5 or more (except *peninsularis* in which there are apparently 3 to 5 setae); color of dorsal scales differing with the species; striae lines on elytra not sharply defined, frequently interrupted here and there by the encroachment of the scales; elytral setae slanting, suberect and conspicuous in some species; eyes smaller and more strictly lateral (fig. 9), the interocular distance considerably more than the greatest diameter of eye (only slightly greater in *peninsularis*); antennal scape surpassing eye; scutellum usually densely scaly; last abdominal sternite of male not emarginate at apex, except in *impressifrons*; hind tibia of male without a brush of long, prominent setae. 3
2. Elytra with striae lines sharply defined, elytral setae short, prostrate, very inconspicuous; femora each with a small tooth; eyes large, partly dorsal (fig. 1), interocular distance equal to or less than the greatest diameter of eye; scales on pronotum elongate; usually transversely directed at least medially; scutellum not densely scaly; last abdominal sternite of male emarginate apically (fig. 5), lower face of hind tibia of male flattened in distal half, the anterior edge of which is set with a brush of long, prominent, erect setae (fig. 8). Length 5.3-6.8 mm., width 1.8-2.75 mm. *sericeus* (Schaller)
- 2'. Elytra with striae lines less sharply defined, elytral setae short, bristly, erect, and very prominent; femora without a tooth; eyes smaller, convex, and lateral (fig. 2), the interocular distance considerably more than the greatest diameter of the eye; scales on pronotum rounded and very closely placed; scutellum very densely scaly; last abdominal sternite of male not emarginate apically (fig. 6), hind tibia of male without a brush of long, prominent, erect setae (fig. 12). Length 2.4-3.6 mm., width 1.0-1.7 mm. *hassayampus*, new species
3. Body more slender; dorsal scales distinctly green; elytra at least 4 times as long as the prothorax, elytral setae fine, inconspicuous, and slanting; first funicular segment one-third, or less, longer than 2; antennal scrobe with posterior half scaly and much shallower than anterior half; frons and dorsum of rostrum flattened to broadly impressed (fig. 9); mandibles each with green scales and at least 3 setae; last abdominal sternite of male broadly impressed apically and with its apical edge broadly emarginate (fig. 4). Length 3.7-5.5 mm., width 1.3-2.2 mm. *impressifrons* Gyllenhal
- 3'. Body less slender; dorsal scales not distinctly green, except in *delicatus* from Lower California, elytra distinctly less than 4 times as long as prothorax, elytral setae coarser and, when suberect or slanting, rather conspicuous; first funicular segment relatively longer, from nearly twice to nearly three times as long as second; antennal scrobe with posterior half narrower and more sharply defined than in *impressifrons*, and bare or with only a few scales; front and dorsum of rostrum variable; mandibles with setae but no scales; abdominal sternite 5 of male not impressed or emarginate apically. 4
4. Nasal plate bare, rather shining, triangular, and well defined, its apex produced a short distance up the dorsum of the rostrum in a fine carina; elytral setae very short and not conspicuous, almost prostrate or slanting, those on pronotum scarcely perceptible even in the lateral view; elytra lacking a distinct color pattern, at most (some specimens of *peninsularis*) with vague and often somewhat ill-defined dark spots. Lower California. 5
- 4'. Nasal plate variable, but not so well defined; elytral setae rather long, slanting, and conspicuous, some of those on pronotum, in lateral view, erect and bristling; dorsum of elytra (except *ochreus*) with a distinct color pattern. United States and Canada. 6
5. Dorsal scales green, sometimes with a few intermixed golden scales; nasal plate narrower; mandibles with numerous setae; eye small, its greatest diameter less than distance between eye and anterior margin of prothorax; scutellum densely scaly. Length 3.6-4.7 mm., width 1.4-1.7 mm. *delicatus* (Horn)
- 5'. Dorsal scales predominantly grayish white, more or less thickly intermixed with brownish scales, the latter usually prominent on the elytra forming vague dark patches basally and dark spots or irregular indefinite oblique bars posterior to middle; nasal plate wider; mandibles each with 3 to 5 very fine setae; eye large, its greatest diameter more than the distance from eye to anterior margin of prothorax; scutellum appearing bare, though actually with some very minute setiform scales. Length 3.0-3.6 mm., width 1.2-1.4 mm. *peninsularis* Horn

6. Each mandible with 3 long and usually 2 or 3 short setae; shortest distance between antennal scrobes, measured across dorsum of rostrum, about one-half the interocular distance; scales on dorsum nearly uniform yellow gray, sometimes with a faint greenish tinge, elytra without color pattern; scales along a narrow median line on pronotum abruptly narrower than adjacent scales and directed posteriorly in apical half to two-thirds (fig. 10). Length 3.0–4.0 mm., width 1.4–1.6 mm. *ochreus* Fall
- 6¹. Each mandible with approximately 7–9 setae; shortest distance, across dorsum of rostrum, between antennal scrobes noticeably greater than one-half the interocular distance (fig. 7); elytra with color pattern of which at least the broad posterior band (fig. 13) is nearly always evident; scales along midline of pronotum directed anteriorly (fig. 11) 7
7. First funicular segment scarcely twice as long as second; prothorax as long as wide or nearly so (relatively longer in male than in female); approximately 8 or 9 setae on each mandible; pronotum more convex at middle, disc of elytra with a vague, transverse flattening at basal fourth just behind humeri; elytral color pattern more sharply defined; scutellum usually bordered posteriorly by a line of contrastingly pale scales; abdominal sternite 5 of female tumid in apical half. Length 3.5–4.8 mm., width 1.5–2.0 mm
..... *americanus* Gyllenhal
- 7¹. First funicular segment at least twice as long as second; prothorax transverse (about 10.0 to 8.0); about 7 or 8 setae on each mandible; pronotum usually not so convex at middle, elytra not flattened on disc toward base; elytral color pattern much as in *americanus* but not as strongly contrasting, the broad sutural stripe frequently reduced to a narrow sutural streak, the dark line near base of the fourth interval usually absent; scutellum not bordered by contrasting pale scales; abdominal sternite 5 of female rather flat to moderately convex, but not tumid in apical half. Length 3.0–4.0 mm., width 1.4–1.8 mm. *decoratus* Woodruff

The following data are limited almost wholly to distributional information, with the exception of that a more complete description is given for *P. hassayampus*, new species. The letters enclosed in parentheses indicate the collection in which the material examined is housed, as follows: National Museum (USNM); C. A. Frost (CAF); Entomological Collection, Department of Zoology and Entomology, The Ohio State University (OSU); E. L. Sleeper (ELS).

Polydrusus sericeus (Schaller)

Framingham and Natick, Mass., C. A. Frost, (CAF, USNM, ELS); Stamford, Conn., A. Estler, (USNM); Chittenden, N. Y., Dicke, (USNM); Brethier, Que., (W. J. Brown, in *lit.*); Ashtabula, Lake and Geauga Co., Ohio, N. J. & E. L. Sleeper, (ELS); Ashtabula Co., Ohio, L. W. & R. T. Everly, (OSU, ELS); near Indianapolis, Ind., Harold Morrison, teste Blatchley & Leng; Dunes St. Pk., Indiana, E. L. Sleeper, (ELS); East Lansing, Michigan (USNM).

Polydrusus hassayampus, new species

Male.—Elongate-oblong; dark reddish brown with legs and antennae pale reddish brown, the color of the legs concealed by the dense coat of scales; all but mandibles, nasal plate, antennae and tarsi densely clothed with rounded, overlapping metallic green scales and with coarse, erect, clavate white scales which, on the elytra, are uniserially arranged on the elytral intervals.

Rostrum as long as head; nasal plate broad, triangular, prominently defined by an elevated ridge; a broad groove behind the nasal plate on dorsum of rostrum, extending to near middle of frons. Mandibles lacking vestiture except for two or three long erect setae. Antennal insertion visible from above, scrobes strongly bent beneath some distance from the eye. Antennal scape small, scarcely attaining hind margin of eye; first funicular segment robust and elongate, second shorter, not as robust, slightly longer than third, fourth to seventh more or less moniliform. Club elongate, acuminate and densely pubescent. Eyes strongly convex, coarsely granulated, the smallest interocular distance one and three-fourths times longest diameter of the eye.

Prothorax one-fourth wider than long, almost parallel sided, the base slightly, if any, wider than the apex. Scutellum rounded, densely clothed with overlapping green scales.

Elytra wider at base than prothorax, the base slightly sinuate; sides gradually divergent to beyond middle then rounded to apex; striae feebly impressed, obscured by scales, striae punc-

tures large, deep, rounded and very close-set, but appear small and widely separated because of the overlapping scales; intervals flattened.

Ventral side densely clothed with rounded overlapping scales; the abdominal sternites, when denuded, very finely crenulate. Fifth sternite strongly rounded apically. Femora unarmed. Length 2.4 mm., width 1.0 mm.

Female.—Differing only from the male in that the first and second abdominal sternites are slightly more swollen. Length 3.4 mm., width 1.4 mm.

Type locality.—Constellation, Yavapai Co., Arizona (along Hassayampa Cr.).

Type material.—Holotype (#66), male, allotype, female, 4 male and 14 female paratypes all from the type locality, VIII-22-42, C. W. Jones, (ELS). Length of paratypes 2.5-3.6 mm., width 1.1-1.7 mm.

Of the North American species, *hassayampus* resembles *delicatulus* (Horn) very closely in form and color, but the latter lacks the very prominent erect setae over the whole of the body, and has the legs clothed with pink to reddish brown scales while in *hassayampus* the legs are clothed with green scales and are noticeably paler than the rest of the body. In *hassayampus* the rostrum is also much shorter and broader. It is apparently more closely related to *P. pallidiseta* Champion from Mexico, differing from that species in the coarser, erect setae on the elytra, the parallel-sided prothorax and the densely clothed legs. *P. pallidiseta* has the prothorax with sides feebly rounded, and the legs reddish brown, very sparsely clothed with greenish scales and erect whitish setae.

There are fifteen examples in (ELS) from Fortuna Mine, Arizona, VIII-13-42, C. W. Jones, which are probably this species, but differ in larger size and much paler vestiture. They are not included as a part of the type series.

***Polydrusus impressifrons* Gyllenhal**

New Haven, Conn.; Ithaca, Albany, Rochester, Seneca Falls, Geneva and Wyoming, N. Y., (USNM); Honeoye Falls, N. Y., (USNM, ELS); Perry (Lake Co.), Ohio, J. S. Houser, (USNM, ELS); Oakland Co., Mich., (USNM).

This species was found in small numbers on willow and Lombardy poplar in the company of *Phyllobius oblongus* (L.), at Perry, Ohio.

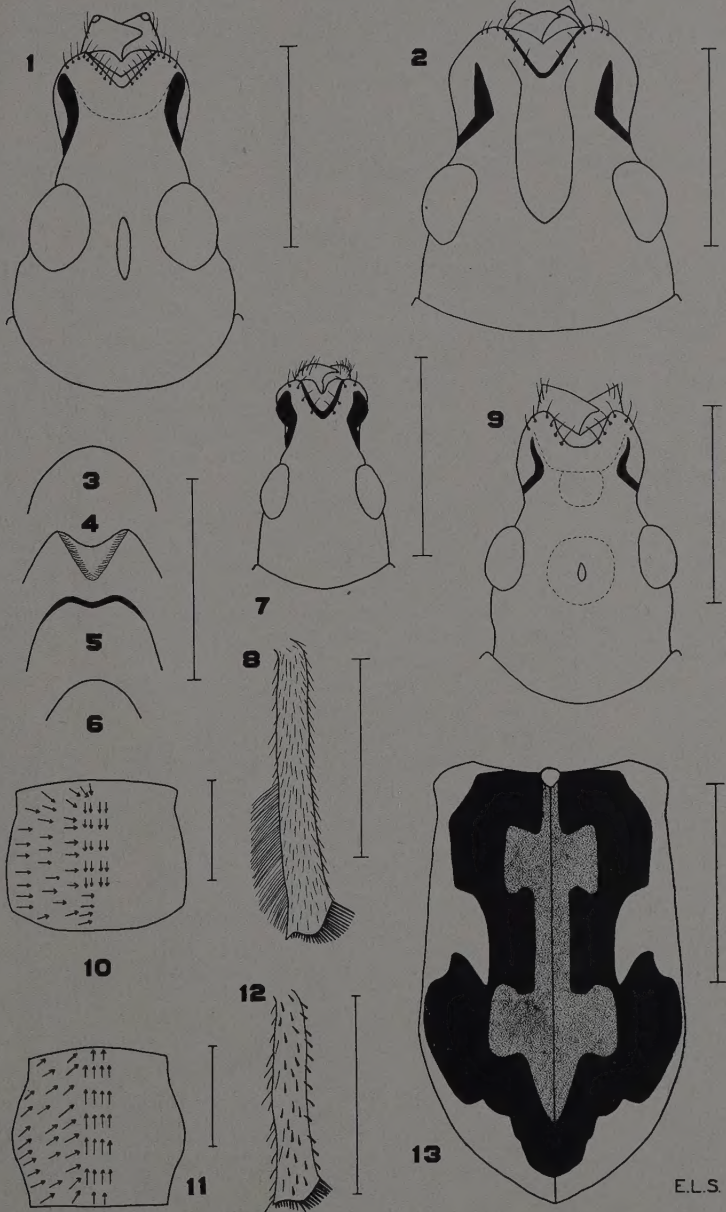
***Polydrusus delicatulus* (Horn)**

San Jose del Cabo, lower California, (USNM, Philadelphia Academy of Sciences), fifteen specimens.

EXPLANATION OF FIGURES IN PLATE

1. Outline of head and rostrum of *Polydrusus sericeus* (Shaller).
2. Same of *P. hassayampus*, new species.
3. Outline of apex of fifth abdominal sternite of *P. americanus* Gyllenhal.
4. Same of *P. impressifrons* Gyllenhal.
5. Same of *P. sericeus* (Schaller).
6. Same of *P. hassayampus*, new species.
7. Outline of head and rostrum of *P. americanus* Gyllenhal.
8. Hind tibiae of *P. sericeus* (Schaller), male.
9. Outline of head and rostrum of *P. impressifrons* Gyllenhal.
10. Outline of prothorax of *P. ochreus* Fall, arrows indicating direction of vestiture on surface.
11. Same of *P. americanus* Gyllenhal.
12. Hind tibiae of *P. hassayampus*, new species.
13. Outline of elytra showing color pattern of *P. americanus* Gyllenhal.

Figures 1, 3 to 9, and 13. Line = 1 mm.
Figures 2, 10 to 12. Line = $\frac{1}{2}$ mm.



***Polydrusus peninsularis* Horn**

Santa Rosa, lower California, (USNM); Santa Rosa, lower California, G. Beyer, (USNM, ELS); San Jose del Cabo, El Taste, Coral de Piedre, lower California, (Philadelphia Academy of Sciences).

***Polydrusus ochreus* Fall**

Cloudcroft, New Mexico, W. Knaus, (USNM), fifteen specimens.

***Polydrusus americanus* Gyllenhal**

Ithaca, Orangeburg, Buffalo, and Otsego Co., N. Y., (USNM); Albany, N. Y., (ELS); Harrisburg, Pa., (ELS); Oakland, Md., (USNM); Washington, D. C., (ELS); Fort Pendelton, W. Va., (USNM); Hamilton Co., Ohio, (Dury Collection); Greene and Franklin Co., O., (OSU, ELS); Ashland, Delaware, Geauga, Hocking, and Putnam Co., O., (ELS); Columbiana, O., (USNM); Athens Co., O., (Ohio University); Elizabeth, Ill., (Illinois St. Nat. Hist. Sur.) and Willow Springs, Ill., (USNM); Ann Arbor and Grand Ledge, Mich., (USNM); "Wisc.", (USNM); St. Louis, Mo., (ELS); Prince Edward Co., Ont., (USNM); Montreal and Quebec, Que., (USNM).

In Ohio this species has been beaten from oak, several species of maple, sycamore, hop-hornbeam, and blue beech.

***Polydrusus decoratus* Woodruff**

Hazen, Ala., (4 paratypes), (USNM); Cliff Cave (St. Louis), Mo., (USNM); Riley Co., and Topeka, Ks., (USNM); Weeping Water and Nebraska City, Nebr., (USNM).

The 4 paratype specimens from Alabama have the elytral setae slightly shorter and the nasal plate somewhat better defined than in the midwestern specimens, indicating possible geographic variation. Further conclusions in this regard will be dependent on more complete distributional information.

LITERATURE CITED

- Blackwelder, R. E. 1947. Checklist of the Coleopterous insects of Mexico, Central America, the West Indies, and South America. USNM Bull. 185(5): 765-925.
- Blatchley, W. S. and C. W. Leng. 1916. Rhynchophora or Weevils of North Eastern America. Nature Publishing Co., Indianapolis. 682 pp.
- Britton, W. E. 1934. Another European weevil in Connecticut. Conn. Exp. Sta. Bull. 360: 474.
- Champion, G. C. 1911. Coleoptera, Rhynchophora (Otioryhynchinae alatae only). Biologia Centrali-Americana 4(3): 178-344.
- von Dalla Torre, K. W. and M. and F. van Emden. 1936. Coleopterorum Catalogus. 27(pt. 147): 1-132.
- Fall, H. C. and T. D. A. Cockerell. 1907. The Coleoptera of New Mexico. Trans. Amer. Ent. Soc. 33: 145-272.
- Frost, C. A. 1946. *Polydrusus sericeus* Schall. (note). Psyche 53: 51.
- Gyllenhal, L. 1834. (In Schönherr) Genera et species Curculionidum. 2(1): 1-326.
- Horn, G. H. (w. LeConte) 1876. The Rhynchophora of America north of Mexico. Proc. Amer. Phil. Soc. 15: 1-455.
- . 1894. The Coleoptera of Lower California. Proc. Cal. Acad. Sci. Series 2. 4: 302-499.
- Kuschel, G. 1950. Nuevos Brachyderinae y Magdalinae Chilenos (Coleoptera, Curculionidae). Arthropoda 1 (2/4): 181-195.
- . 1955. Nuevas sinonimias y anotaciones sobre Curculionoidea (1). Rev. Chil. Ent. 4: 261-312.
- Pierce, W. D. 1909. Studies of North American weevils. Proc. USNM 37: 325-364.
- Schaller, J. G. 1783. Neue Insecten beschrieben. Schrift. naturf. Ges. Halle, I. pp. 217-328.
- Woodruff, L. B. 1923. A new species of *Polydrusus*. Jour. N. Y. Ent. Soc. 31: 155-157.

CYTOPLASMIC INHERITANCE OF PLASTIDS IN *IMPATIENS SULTANII* HOOK, F., *PETUNIA* *VIOLACEA* LINDL. AND *CHLOROPHYTUM* *ELATUM* R. BR.¹

K. K. PANDEY AND GLENN W. BLAYDES

Department of Botany and Plant Pathology, The Ohio State University, Columbus 10

INTRODUCTION

The inheritance and mode of chlorophyll distribution in variegated plants have long attracted the attention of botanists. It is probable that most variegated varieties of plant species, domesticated and wild, are somatic, mutant individuals which appear as chimeras (Blaydes, 1953). Many of these may be propagated vegetatively and persist indefinitely through the aid of man. However, the understanding of the processes involved in the structure and inheritance of leaf variegation is still far from complete.

A favorable condition for the study of chlorophyll inheritance is found in plants where one or more shoots are completely albino. Such shoots are incapable of independent existence, except when under special cultural methods, and may be found as mutants or somatic segregates on green or variegated plants (Blaydes, 1953). The most frequent occurrence of such albino mutants is found in periclinally, mericlinally and sectorially variegated plants. Since flowers on albino shoots are frequently unable to produce seed normally, mericlinial, periclinial, or sectorial chimeras are generally used for genetical experiments. As the reproductive cells are derived from the sub-epidermal layer of the shoot, the second layer of the shoot apex must be regularly albino if the genetic data from crosses in such plants are to be relied upon. Sectorially variegated plants in which the histogenic tissues are constantly rearranging are not reliable for genetic studies on variegation. Periclinally variegated plants, on the other hand, are histogenically much more stable and are satisfactory material for such investigations. A large number of periclinally variegated plants in which histogenic layers, L-II in Dicots, or L-II and L-III in Monocots (Dermen, 1947; Imai, 1935), are albino is available in nature. The present study has been carried out upon periclinally variegated plants of *Chlorophytum elatum* R. Br. and *Impatiens sultanii* Hook. f.

Types of Plastid Inheritance

Mendelian.—In a large number of plants albino seedlings appear in the progeny of the heterozygous parent which carries the recessive albino gene. Albino seedlings which die soon after germination have been found to segregate in a simple Mendelian ratio in *Antirrhinum latifolium* and *Melandrium album* (Baur, 1910), *Zea mays* (Lindstrom, 1918; Beadle, 1929), *Hordeum distichum* (Kiessling, 1918), *Phaseolus vulgaris* (Tjebbes and Kooiman, 1919), *Eleusine indica*, *Sorghum* species, *Eleusine coracana*, *Pennisetum typhoides*, *Setaria italica* and *Paspalum scrobiculatum* (Rangaswamy Ayyangar *et al.*, 1931, 1932, 1935, 1936), *Oryza sativa* (Ramiah *et al.*, 1935), *Coleus blumei* (Rife, 1948) and others. Mendelian segregations of pale green or yellowish green seedlings have been reported in *Urtica pilulifera* (Correns, 1909), *Ipomoea hederacea* (Mizazawa, 1918), *Mirabilis jalapa xantha* (Correns, 1918), *Zea mays* (Lindstrom, 1918), *Nicotiana rustica* (Allard, 1919),

¹Department publication number 601, Department of Botany and Plant Pathology, The Ohio State University.

Pelargonium species (Chittenden, 1926), *Oryza sativa* (Ramiah *et al.*, 1935), *Secale cereale* and *Eleusine coracana* (Ramiah *et al.*, 1935), *Sorghum* species, *Setaria italica* and *Paspalum scrobiculatum* (Rangaswamy Ayyangar *et al.*, 1935, 1941), *Hordeum vulgare* (Smith, 1951), *Allium cepa* (Yarnell, 1954), *Coleus blumei* (Boye and Rife, 1938) and others. Various types of chlorophyll variegations have also been shown to segregate as simple Mendelian recessives in *Lunaria* (Correns, 1909), *Aquilegia vulgaris* (Baur, 1918), *Pisum arvense* (*P. sativum*) (Rajanus, 1918), *Capsella bursa-pastoris* and *Arabis albida* (Correns, 1919), *Hordeum vulgare* (Imai, 1936), *Oryza sativa* (Jodon, 1940), *Coleus blumei* (Pandey, unpublished) and others. However, Kempton (1924) found albinism dominant to green in maize. Inheritance of variegation governed by nuclear factors is also found in *Antirrhinum* sp. (Baur, 1910), *Zea mays* (Beadle, 1929), *Urtica peraurea*, *Mirabilis jalapa variegata*, *Pelargonium chlorina* (cited by Sansome and Philp, 1939) and other species.

Non-Mendelian.—Non-Mendelian inheritance may be of two types: (1) Biparental — in which the hybrid character is contributed by both male and female parents, and (2) Maternal — in which the character in question is controlled by the female parent only.

In variegated varieties of *Pelargonium zonale albomarginata*, *Antirrhinum majus albomaculata*, *Aquilegia vulgaris* (Baur, 1909, 1918) and *Oenothera* species (Stomps, 1917, cited by Scherz, 1927) there are plants in which some branches are solid white and some solid green in addition to periclinally variegated branches. Selfed flowers on these solid green and white branches produce progeny which are similar to their parent branch. But when flowers on the green and white branches are crossed reciprocally the hybrid seedlings are always "mosaic" (containing green and white sectors), regardless of the way the cross was made. The same phenomenon is repeated if flowers on solid green and white branches in any of the hybrid plants are crossed. Baur explained this on the basis that in these cases the cytoplasmic plastids, not the nucleus, was responsible for the hybrid character and that the cytoplasmic plastids were contributed by both the parents in these species. An almost similar situation has been found in variegated races of *Capsicum annum* (Ikeno, 1917).

The earliest case of maternal inheritance was described by Correns (1909) in *Mirabilis jalapa albomaculata*. Plants of this strain produced branches which had solid green or solid white leaves and also branches with variegated leaves. Selfed seedlings of completely green and white branches were green or white, respectively. Crosses between flowers on green and white branches always produced progeny which resembled the mother parent. No trace of any influence by the male parent was visible. Correns explained this maternal inheritance on the basis of cytoplasmic "disease" giving rise to the defective plastids in the albino parent. He assumed that the cytoplasmic contribution of the male parent was negligible and the zygote contained only the cytoplasm of the female parent. A similar situation was found by Baur (1910) in *Antirrhinum majus albomaculata* and *Aquilegia vulgaris* and also by Gregory (1915) in *Primula sinensis*. However, these workers thought that the "diseased" plastids themselves and not the "diseased" cytoplasm, were responsible for conveying the defective plastids from the mother to the progeny. According to these investigators, the young progeny of a branch with both kinds of plastids will give rise to variegated branches. This may be brought about by segregation of the plastids during somatic mitoses. Since these earlier reports, maternal inheritance of plastids has been found in a large number of species distributed in a number of genera and families (*Erodium cicutarium*—Scherz, 1927; *Zea mays*—Anderson, 1923; Rhoades, 1943; *Chlorophytum elatum* and *Chlorophytum comosum*—Collins, 1922; *Hydrangea*—Chittenden, 1926; *Arabis*, *Aubretia* and *Mesembryanthemum*—Correns, cited by Chittenden, 1926; *Stellaria media albomaculatus*, *Mercurialis annua*, *Senecio vulgaris*, *Taraxacum*



EXPLANATION OF FIGURES IN PLATE I

1. Stable clone of variegated *Chlorophytum elatum* form *medio-variegata*.
2. Unstable seedling clone of variegated *Chlorophytum elatum* producing pure green and albino shoots as well as variegated shoots. Generally the color of the flowering shoot resembles that of the central area of the leaf at its base. The bracts on the flowering shoot normally bear the same variegation pattern as is common in the leaves.
3. Albino and variegated (mutant) seedlings of *Chlorophytum elatum* from the selfed seeds of *medio-variegata* form.
4. Albino seedlings of *Impatiens sultanii* from the cross, variegated \times green.

officinale, *Hieracium auricula*, *Urtica pilulifera*, and *Trifolium pratense*—cited by Scherz, 1927; *Hosta japonica*—Yasui, 1929; *Rhodeo japonica*, *Dendrobium* and *Habenaria*—Imai, 1935, from personal information from breeders, conclusions drawn probably from the results of selfing only; *Humulus*, *Pelargonium vars.* and *Melandrium album*—Sansome and Philp, 1939; *Triticum vulgare*—Umar, 1943; Pao and Li, 1946; Arnason, 1956; *Hordeum vulgare*—Arnason, Harrington and Friesen, 1946; Imai, 1928; *Sorghum* and *Phaseolus*—Snyder, 1951). In *Avena sativa*, Robb (cited by Ramiah *et al.*, 1935) reported an interesting case of maternal inheritance of variegation in which variegated plants had only striped progeny with occasional green plants but no albinos.

In certain cases inheritance of plastids may not be clear cut, for maternal plastid inheritance in these cases may be complicated by one or more accompanying phenomena such as gene segregation and plastid mutation (Imai, 1928; Rhoades, 1943).

MATERIALS AND METHODS

***Impatiens sultanii*.**—Periclinally variegated plants of *Impatiens sultanii* have white bordered leaves. Histogenically, the L-II is albino (Pandey, unpublished). These plants also may bear branches which are albino (fig. 5). Flowers borne on the albino branches are cleistogamous and abscise before opening. Attempts to pollinate the flowers by cutting open well-developed flower buds failed to produce fruits. Therefore, flowers which appeared "normal" and were borne on the variegated branches were used for pollination.

In *I. sultanii*, natural self-pollination from the pollen of the same flower is impossible. At the time of anthesis, stigma is tightly capped by a fleshy androecium. The androecium dehisces from the groove in the outer surface of the cup, usually within 12 hours after flower opening and rarely before the flower is fully open (fig. 6). About 3 to 5 days after androecium dehiscence, the androecium cup dries and drops off, leaving the immature stigma exposed (fig. 7). Twenty-four to thirty-six hours elapse before the stigma is fully developed, open and receptive to pollen (fig. 8). Pollination before this stage of the flower is unfruitful.

***Chlorophytum elatum*.**—Occasional variegated seedlings have been obtained from selfed variegated plants under greenhouse conditions (fig. 2). Comparatively stable *albo-marginata*, *medio-variegata* and *medio-albinata* forms (Imai, 1935) were easily obtained from these variegated plants. Generally the color of the flowering shoot resembles that of the central area of the leaf at its base. The bracts on the flowering shoot normally bear the same variegation pattern as is common in the leaves. Only stable forms of variegated plants (fig. 1) were used for cross pollination with pure green plants. Flowers were emasculated on the evening prior to flower opening. A description of various variegated plants used in this experiment is given in table 1.

***Petunia violacea* Lindl.**—A single pink flowering plant of *Petunia violacea* having a variegated branch was found among a large group of normal green seedlings. The variegation in this branch was irregular and patchy (fig. 9). However, many flowers were available from solid or almost solid albino regions of the branch. A few flowers were also observed in which, out of 5 sepals, 2 or more were albino while the remaining ones were pure green or variegated.

P. violacea is a self-incompatible species (Mather, 1943). The flowers on pure green branches and the variegated branch of this plant were crossed reciprocally with another normal green, violet flowered plant. No emasculation in these flowers is necessary. However, only the flowers in which the shiny, receptive stigma was free from pollen, were chosen for cross-pollination. Anthers were removed from flowers before pollination.



EXPLANATION OF FIGURES IN PLATE II

5. Variegated plant of *Impatiens sultanii*. An albino shoot with cleistogamous flowers can be seen at the base of the stem.
6. The pistil of *Impatiens sultanii*. At the time of anthesis, stigma is tightly capped by a fleshy androecium. The androecium dehisces from the groove in the outer surface of the cup, usually within 12 hours after flower opening and rarely before the flower is fully open.
7. The pistil of *Impatiens sultanii* showing exposed immature stigma. About 3-5 days after androecium dehiscence, the androecium cup dries and drops off, leaving the immature stigma exposed.
8. The pistil of *Impatiens sultanii* showing mature stigma. Twenty-four to thirty-six hours after the dropping of the androecium cup the stigma is fully developed, open, and receptive to pollen.
9. Unstable plant of *Petunia violacea* giving rise to a few variegated shoots.

TABLE 1

Description of variation in albo-marginata, medio-albinata and medio-variegata forms of Chlorophytum elatum

Plant No.	Plant Type (Form)	Description of variation in leaves and flowering shoot
V	<i>Albo-marginata</i>	Fully green except for a narrow border which is yellow; flowering shoot green.
IX	<i>Albo-marginata</i>	Fully green except for a narrow border which is light green; flowering shoot green.
III	<i>Medio-albinata</i>	Center greenish yellow with light green streaks evenly distributed and border light green; flowering shoot yellow.
IV	<i>Medio-albinata</i>	Center yellow with few green streaks and border fully green; flowering shoot yellow.
X	<i>Medio-albinata</i>	Center yellowish green with few green streaks and border fully green; flowering shoot yellow (Reverse of Plant No. IX).
II	<i>Medio-variegata</i>	Center yellowish green with numerous greenish yellow streaks and border greenish yellow; flowering shoot yellowish green with many yellow streaks.
VIII	<i>Medio-variegata</i>	Center greenish yellow with fine green streaks as well as broad green stripes and border green; flowering shoot yellow with broad green stripes.
I	Normal green	Fully green, normal; flowering shoot green.
VI	Normal green	Light green, occasional yellowish green streaks in some leaves; flowering shoot green.
VII	Normal green	Light green, normal; flowering shoot green.

RESULTS

Impatiens sultanii.

Since variegated plants of this species are pollen sterile, only the result of one way cross, using the variegated plant as the female parent (variegated \times green) is available (fig. 4). The color of the hybrid seedlings is as follows:

Cross	No. of seeds sown	No. of seedlings germinated		
		Albino	Green	Variegated
Variegated \times green	83	26	0	0

The subepidermal layer in this variegated plant has been found to contain only albino plastids. Thus, only plastids from the germinal tissue of the female parent are represented in hybrid seedlings.

Chlorophytum elatum.

Albo-marginata, *medio-variegata* and *medio-albinata* forms of this species were selfed, crossed reciprocally among themselves and some were also crossed reciprocally with normal pure green plants. Seeds obtained after selfing or crossing were

collected separately and sown separately for each capsule and the observations on the color of seedlings were recorded. The number of yellow, green or variegated seedlings obtained in various crosses are given in table 2.

It may be inferred from table 2 that the color of the progeny is almost entirely governed by the female parent (fig. 3). The progeny of plant IV which gives rise only to yellow seedlings, regardless of the type of cross, confirm this inference. The progeny of pure green forms are all green. *Albo-marginata* forms also produce

TABLE 2
Number of yellow, green or variegated seedlings obtained
in various crosses of *Chlorophytum elatum*

Female Parent No.	Male Parent	No. of seeds sown	No. of seeds germinated	No. of Seedlings			Nature of Maternal Plastids	Percentage of seedlings with mutated plastids
				Yellow	Green	Variegated		
II <i>Medio-variegata</i>	II	45	32	31	0	1	Yellow	3.1
	I	12	11	11	0	0		0
	III	34	24	14	0	10		41.6
	V	15	10	8	1	1		20
} 16.9								
III <i>Medio-albinata</i>	III	19	18	18	0	0	Yellow	0.0
	IV	12	12	12	0	0		
IV <i>Medio-albinata</i>	IV	95	69	69	0	0	Yellow	0.0
	III	15	15	15	0	0		
	VI	17	13	13	0	0		
	IX	30	26	26	0	0		
V <i>Albo-marginata</i>	V	16	15	0	15	0	Green	0
	IV	12	11	0	10	1		9
} 3.8								
VI Green	VI	26	16	0	16	0	Green	0.0
	IV	15	14	0	14	0		
VII Green	VII	11	11	0	11	0	Green	0.0
VIII <i>Medio-variegata</i>	VIII	19	15	3	6	6*	Yellow	80
	VII	12	12	12	0	0		0
	IV	26	16	11	2**	3		31.2
} 39.5								
IX <i>Albo-marginata</i>	IX	39	22	0	22	0	Green	0
	IV	42	32	1	28	3		9.7
} 5.6								
X <i>Medio-albinata</i>	X	18	12	12	0	0	Yellow	0.0
	IX	38	22	22	0	0		

* Of these, three later became fully green.

** Both of these became variegated.

almost all green seedlings. The progeny of *medio-albinata* forms are all yellow. Most of the *medio-variegata* progeny are also yellow; however, there are some fully green or variegated seedlings. Thus, genetically there are three forms: 1) Pure green and *albo-marginata* which produce green seedlings, 2) *Medio-albinata* which produces yellow seedlings, and 3) *Medio-variegata* which produces mostly yellow seedlings with some green and variegated ones.

The mutation rate varies greatly from plant to plant. Most of the mutants arise in the progeny of *medio-variegata* forms. Also the mutation rates in the two

medio-variegata plants are obviously different. In *medio-albinata* and *albo-marginala* forms, the mutation rate is negligible. There are streaks on the leaves of *medio-variegata* forms which appear abruptly and are not connected with the base of the leaf. This indicates that such streaks are formed as the result of mutations in the early ontogeny of the leaf. If this is the case, it may be expected that such parents will have a high rate of mutation.

TABLE 3

Number and kinds of seedlings obtained from different crosses in *Petunia violacea*. The plant with a variegated shoot had pink flowers. The variegated shoot had 3 variegated branches (Br. 1, Br. 2 and Br. 3). Pink flowers on variegated and green shoots were crossed reciprocally with violet flowers on a pure green plant. All flowers used from variegated branches had only albino sepals, unless otherwise stated

Cross No.	Cross (♀ × ♂)	No. of Seeds Sown	No. of Seedlings Germinated		
			Albino	Green	Variegated
I Group	(August 5, 1956)				
(1)	Pink Var. Br. 1 × Violet Gr.	217	176	7	4*
(2)	Pink Var. Br. 1 × Violet Gr.	200	154	6	9*
II Group	(September 16-19, 1956)				
(3)	Pink Var. Br. 1 × Violet Gr.	279	154	0	0
(4)	Pink Var. Br. 2 × Violet Gr.	83	59	0	0
(5)	Pink Var. Br. 3 × Violet Gr. (All sepals greenish white)	260	159	0	0
(6)	Pink Var. Br. 3 × Violet Gr.	237	159	0	0
(7)	Pink Var. Br. 1 × Violet Gr. (2 sepals albino and 3 green)	195	0	182	0
(8)	Violet Gr. × Pink Var. Br. 2	365	0	232	0
(9)	Violet Gr. × Pink Var. Br. 2	315	0	210	0
(10)	Violet Gr. × Pink Gr.	324	0	280	0
(11)	Pink Gr. × Violet Gr.	252	0	120	0

*Out of four and nine variegated seedlings from crosses (1) and (2), one and eight seedlings, respectively showed variegation starting from the cotyledonary leaves; in the remaining seedlings, variegation appeared in later leaves.

In *medio-variegata* plant II there seems to be a tendency to produce more mutants in the progeny from the cross with plant III than by selfing. Conversely, in the cross with a different male parent (plant V) the mutation rate seems to have declined. In *medio-variegata* plant VIII, selfing produces a very high percentage of mutants (80%). In the cross with plant IV the percentage of mutants declines considerably (31.2%). In the cross with plant VII there are no mutants. These observations indicate that mutation rate in the zygote is affected by the male

parent. Apparently no plastids pass from the pollen to the zygote, as is evident from the cross in plant IV. It may be assumed that no male cytoplasm enters the egg at the time of fertilization. The influence of the male parent, therefore, must be exerted through the nuclear elements. The effect of the male parent appears to be different with the resultant different genetic constitution of the zygote.

***Petunia violacea*.**

The single variegated shoot on the one plant gave rise to several small branches which bore flowers. Flowers on three of these branches, designated as Br. 1, Br. 2 and Br. 3, were used for cross pollination. Most of these flowers had nearly complete albino sepals, but a few of them had 2 or more entirely green or variegated sepals. Seeds of individual fruits were collected and sown separately.

Two sets of crosses were made about 45 days apart. The first group of crosses was made on August 5, 1956, and the other during the period September 16-19 as flowers opened. Mature fruits were harvested about a month after pollination in both crosses. The number and kinds of seedlings obtained from these crosses are given in table 3.

From group II crosses it is evident that seeds from flowers with all albino sepals gave rise only to albino seedlings when crossed with normal flowers on green shoots. Flowers on green shoots, when pollinated with pollen from flowers on variegated shoots, gave rise only to green seedlings. In cross (7) where the female flower had 2 albino sepals and 3 green, all resultant seedlings were green. Apparently the albino tissue did not include the germinal tissue from which the eggs arose.

It should be noted that no mutants arose from any cross in group II, whereas both crosses in group I resulted in some mutant progeny. However, 92.6 percent of the seedlings in group I crosses were albino. Some of the variegated seedlings had apparently green cotyledonary leaves but variegation appeared in later leaves.

DISCUSSION

The results of crosses between pure green and variegated chimeral plants in *Impatiens sultanii*, *Chlorophytum elatum* and *Petunia violacea* clearly suggest that plastid inheritance in these plants is strictly maternal. The cross between periclinally variegated and pure green plants in *I. sultanii* gave only albino seedlings. However, some of the reciprocal crosses between green and variegated plants of *C. elatum* and *P. violacea* gave rise to seedlings of maternal plastid color and also a few variegated and solid mutant (yellow or green) seedlings.

Collins (1922) reported maternal inheritance of plastids in *C. elatum* and *C. comosum* but he ascribed the appearance of variegation to "some peculiar action which brings about a somatic segregation of the two opposite characters and the disorderly distribution to leaves . . . upon the sequence and mode of subsequent meristematic segregation." Since Collin's hypothesis, we have come to a much better understanding of the origin and structure of chimeras and variegations. Many of the stable forms of variegation in *C. elatum* and other species are known to be periclinal chimeras and the relationship between their chimera structure and hereditary behavior is easily understood.

There is a large difference in the percentage of mutants observed in the progeny of different plants. This indicates a genetical basis for the rate of plastid mutation. Most of the mutants in *C. elatum*, however, arose in the *medio-variegata* forms. There seemed to be a positive correlation between the number of streaks and stripes on the leaves and the number of mutant seedlings produced in their progeny. The two *medio-variegata* plants are periclinal chimeras; in plant II, the

first and second layers are yellow and the third layer green; and in plant VIII, the epidermis is green and the second and third layers yellow (Pandey, unpublished). As most of the broad stripes in the central region of the leaf in plant VIII seem to be connected with the epidermal layer which forms the border, it appears that stripes generally arise because of the occasional participation of the epidermis in the formation of deeper layers in the central area of the leaf. If it is presumed that mutant seedlings are produced because of the occasional replacement in the floral primordia, of the cells of histogenic layer L-II by the different kind of cells derived from the transverse division of the epidermal cells above, the increased number of mutant seedlings could be easily explained. On this hypothesis however, no variegated seedlings should appear in the progeny but only solid green or yellow. As variegated seedlings with variegated cotyledonary leaves do appear in the progeny, this hypothesis seems untenable.

There are many narrow streaks on the leaves which do not appear to be connected with the epidermal layer and which may have originated as mutations in color of the plastid in the early ontogeny of the leaf. It would have been easy to explain the occurrence of fine streaks as well as broad stripes on the leaves and the high number of mutants in the progeny on the basis of high rate of plastid mutation in these plants, but this does not fit with observations that: 1) broad stripes do not occur evenly in the entire leaf but are concentrated in the central area of the leaf and, 2) most of the broad stripes seem to be connected with the upper epidermal layer.

A high mutation rate of plastids combined with occasional replacements of the cells of the germinal layer by cells from the epidermal layer provide a most probable explanation for the appearance of a large number of mutant seedlings in the *medio-variegata* plants. The facts that the majority of the mutant seedlings (92.3%) in plant II, where there are only fine streaks but no broad stripes, are variegated and that plant VIII, which had broad stripes as well as fine streaks, produces variegated and also a number of solid green mutant seedlings support this hypothesis.

In *C. elatum*, the mutation rate of plastids in the zygote seems to be affected by the genetic constitution of the male parent. Ramiah *et al.* (1935) observed a higher percentage of chlorophyll defective seedlings in hybrid generations than in pure lines of rice.

In discussing maternal inheritance of leaf variegation in wheat, Arnson (1956) assumes that "since variegated plants have both normal and mutated plastids, it is possible that plastid segregation results in some eggs having only normal, some having mixed, and some only mutant plastids." This is difficult to accept since no one to date has clearly demonstrated two kinds of plastids in the same cell of a *mature* variegated plant. It is believed that the occurrence of variegated seedlings in the progeny of a plant showing maternal inheritance of plastids is due to the mutation of plastids in the egg or zygote. The segregation of two kinds of plastids into two distinct tissues takes place in the embryogeny of the seed. Upon selfing a variegated plant, Arnason did not get any albino seedlings but only green or variegated. This was explained by Arnason as being due to the high rate of back mutation from albino to green plastids. The same phenomenon may explain the result of Robb (1933, cited by Ramanujam *et al.*, 1935) in *Arena sativa*. He found maternal inheritance of variegation, with selfed seedlings of variegated plants giving rise only to striped progeny with occasional green plants but no albinos.

Winge (1919), after reviewing the literature on variegated plants, presented a hypothesis in which he postulated that the physical basis of non-Mendelian inheritance might lie in plastids or cytoplasm. If it were in plastids, a variegated plant would produce albino, green or variegated progeny according to the kinds

of plastids present in the zygote; but if the physical basis for variegation was cytoplasm, all the progeny of a variegated plant would be variegated with no pure green or albino seedlings. In both cases the inheritance might be maternal or biparental according to whether or not in the particular species fertilization contributed the cytoplasm and plastids from the male parent. A large number of cases of maternal and some cases of biparental inheritance have been reported in which the physical transmission of individual kinds of plastids has been supposed to be the basis of the inheritance of variegation. Only two cases (*Capsicum*—biparental, Ikeno, 1917; *Humulus*—maternal, Winge, 1919) have been reported in which the physical basis of inheritance of variegation has been assumed to be the cytoplasm, and not the plastids. It is suggested that this behavior could also be explained on the basis of a high rate of reversible plastid mutation in the particular races of *Capsicum* and *Humulus*.

In the numerous reports of non-Mendelian inheritance it is a significant fact that with the exception of *Antirrhinum majus albo-maculata* and *Aquilegia vulgaris* (Baur, 1909, 1910 and 1918), the two types of hereditary transmissions, maternal and biparental, have not been found to occur in the same species (Randolph, 1922). This suggests that male cytoplasm enters the egg in some species and not in others. It is possible that in the strains of *A. majus* and *A. vulgaris* in which both maternal and biparental inheritance were reported there might be high rate of reversible plastid mutation resulting in each zygote containing both types of plastids. If this were true it might have easily confused the identity of maternal transmission of plastids.

In *Petunia violacea*, in the two crosses made between variegated and pure green plants in summer, some green or variegated mutants were produced but in the crosses made in early autumn no mutants were obtained in hundreds of seedlings. This indicates that mutation rate of plastids varies greatly with photoperiod, light intensity or temperature variations, or both of these. Ramiah *et al.* (1935) also reported seasonal variation in the mutation rate in rice producing albino and other chlorophyll deficient mutants.

SUMMARY

A study of the inheritance of plastids in chimeral plants of *Impatiens sultanii* Hook. f., *Petunia violacea* Lindl. and *Chlorophyllum elatum* R. Br. showed that plastid inheritance in these plants was strictly maternal.

In *I. sultanii* no mutant seedlings were observed in the progeny but in *C. elatum* and *P. violacea* some mutant seedlings were produced.

Different plants of *C. elatum* showed different rates of plastid mutation. However, most of the mutant seedlings were produced in the progeny of the *medio-variegata* plants. This has been explained to be due to (1) a high rate of plastid mutation in the cells and (2) occasional replacement of the cells of histogenic L-II by cells derived by transverse division from the epidermal cells.

In *C. elatum*, the mutation rate of plastids in the zygote seems to be affected by the genetic constitution of the male parent.

There is a strong indication that in *P. violacea* the mutation rate of plastids varies greatly with seasonal variation.

ACKNOWLEDGMENT

The senior author is grateful to the Graduate School of The Ohio State University for the Mary S. Muellhaupt Post-doctoral Fellowship during the tenure of which this study was undertaken. We are both indebted to Mr. A. S. Heilman for the preparation of the Plates.

LITERATURE CITED

- Allard, H. H. 1919. The Mendelian behavior of *aurea* character in a cross between two varieties of *Nicotiana rustica*. Amer. Nat. 53: 234-238.
- Anderson, E. G. 1923. Maternal inheritance of chlorophyll in maize. Bot. Gaz. 76: 411-418.
- Arnason, T. J. 1956. Maternal inheritance of leaf variegation in hexaploid wheat. Canad. Jour. Bot. 34: 801-804.
- Arnason, T. J., J. B. Harrington, and H. H. Friesen. 1946. Inheritance of variegation in Barley. Canad. Jour. Res. 24C: 145-157.
- Baur, E. 1909. Das Wesen und die Erblichkeitsverhältnisse der var. *albomarginata* hort. von *Pelargonium zonale*. Z. indukt. Abstamm.- u. Vererb.-Lehre 1: 330-351.
- . 1910. Vererbungs- und Bastardierungsversuche mit *Antirrhinum*. Z. indukt. Abstamm.- u. Vererb.-Lehre 3: 34-98.
- . 1918. Mutation von *Antirrhinum majus*. Z. indukt. Abstamm.- u. Vererb.-Lehre 19: 177-193.
- Beadle, G. W. 1929. Yellow stripe—a factor for chlorophyll deficiency in maize located in the Pr pr chromosome. Amer. Nat. 63: 189-192.
- Blaydes, G. W. 1953. The romance of domesticated plants. Ohio Jour. Sci. 53: 193-215.
- Chittenden, R. J. 1927. Vegetative segregation. Bibl. Genetica 3: 355-442.
- Collins, E. J. 1922. Variegation and its inheritance in *Chlorophytum elatum* and *Chlorophytum comosum*. Jour. Genet. 12: 1-17.
- Correns, C. 1909. Vererbungsversuche mit blass (gelb) grünen und buntblättrigen Sippen bei *Mirabilis*, *Urtica* und *Lunaria*. Z. indukt. Abstamm.- u. Vererb.-Lehre 1: 291-329.
- . 1918. Zur Kenntniss einfacher Mendelnder Bastarde. II. *Mirabilis jalapa xantha*, und ihre Bastarde. III. *Urtica urens per aurea*. Sitz. der Preuss. Akad. der Wiss. 33: 221-268.
- . 1919. Vererbungversuche mit bunt-blättrige Sippen 1. *Capsella bursa pastoris*, *albovariables* und *chlorina*. Sitz. der Preuss. Akad. der Wiss. 34: 585-610.
- Dermen, H. 1945. The mechanism of colchicine—induced cytological changes in cranberry. Amer. Jour. Bot. 32: 387-394.
- Gregory, R. P. 1915. On variation in *Primula sinensis*. Jour. Genet. 4: 305-321.
- Ikeno, S. 1917. Studies on the hybrids of *Capsicum annum*. II. On some variegated races. Jour. Genet. 6: 201-229.
- Imai, Y. 1928. A consideration of variegation. Genetics 13: 544-562.
- . 1935. Variation in the rate of recurring plastid mutations in *Hordeum vulgare* caused by differences in the sowing times. Genetics 20: 36-41.
- . 1936. Recurrent auto- and exomutation of plastids resulting in tricoloured variegation of *Hordeum vulgare*. Genetics 21: 752-757.
- Jodon, N. E. 1940. Inheritance and linkage relationships of a chlorophyll mutation in rice. Jour. Amer. Soc. Agron. 32: 342-346.
- Kajanus, B. 1918. Über eine konstant gelbunte Pisum-Rasse. Bot. Notiser. 83 84.
- Kempton, J. H. 1924. A dominant lethal chlorophyll mutation in maize. Jour. Agri. Res. 29: 307-309.
- Kiessling, L. 1918. Einige besondere Fälle von Chlorophylldefecten Gersten. Z. indukt. Abstamm.- u. Vererb.-Lehre 19: 160-176.
- Lindstrom, E. V. 1918. Chlorophyll inheritance in maize. Cornell Univ. Expt. St. Memoir 13: 1-68.
- Mather, K. 1943. Specific differences in Petunia. I. Incompatibility. Jour. Genet. 45: 215-235.
- Miyazawa, B. 1918. Studies of inheritance in the Japanese *Convolvulus*. Jour. Genet. 8: 59-83.
- Pao, W. K. and H. W. Li. 1946. Maternal inheritance of variegation in common wheat. Jour. Amer. Soc. Agron. 38: 90-94.
- Ramiah, K. and S. Ramanujam. 1935. Chlorophyll deficiencies in rice (*Oryza sativa*). Proc. Ind. Acad. Sci. 2: 343-368.
- Randolph, L. F. 1922. Cytology of chlorophyll types of maize. Bot. Gaz. 73: 337-375.
- Rangaswamy Ayyangar, G. N. and P. Krishna Rao. 1931. The inheritance of characters in Ragi (*Eleusine coracana* Gaertn.). Part V. Albinism. Ind. Jour. Agri. Sci. 1: 569-576.
- and M. A. Sankara Ayyar. 1935. Chlorophyll deficiencies in *Penisetum typhoides*—Pearl Millet. Madras Agri. Jour. 23: 394.
- and U. Achyutta Warier. 1936. Albinism in *Eleusine indica* Gaertn. Curr. Sci. 5: 301-302.
- et al. 1941. The inheritance of depth of green color in the leaves of *Sorghum*. Madras Agri. Jour. 29: 492.
- Rhoades, M. M. 1943. Genic induction of an inherited cytoplasmic difference. Proc. Nat. Acad. Sci. Wash. 29: 327-329.
- Rife, D. C. 1948. Simply inherited variations in *Coleus*. Jour. Hered. 39: 85-91.
- Sansome, F. W. and J. Philp. 1939. Recent Advances in Plant Genetics. P. Blakiston's, Son & Co. Inc. Philadelphia. pp. 141-159.

- Scherz, W. 1927. Beiträge zur Genetik der Buntblatterigkeit. Z. indukt. Abstamm.- u. Vererb.-Lehre 45: 1-40.
- Sinnot, E. W., L. C. Dunn, and Th. Dobzhansky. 1950. Principles of Genetics. McGraw-Hill Book Company, Inc. New York. pp. 438-448.
- Smith, L. 1951. Cytology and genetics of barley. Bot. Rev. 17: 133-202.
- Snyder, L. H. 1951. The Principles of Heredity. D. C. Heath and Co. Boston. pp. 303-312.
- Tjebbes, K. and H. N. Kooiman. 1919. Erfelijkheidsonderzoekingen bij boonen III. Albinisme. Genetica 1: 532-538
- Umar, S. M. 1943. A case of maternally inherited variegation in wheat. Ind. Jour. Genet. and Pl. Breed. 3: 61-63.
- Winge, O. 1919. On the non-Mendelian inheritance in variegated plants. Compt. Rend. Trav. Labor. Carlsberg. 14(3): 1-20.
- Yarnell, S. H. 1954. Cytogenetics of the vegetable crops. I. Monocotyledons. Bot. Rev. 20: 277-359.
- Yasui, K. 1929. Studies on the maternal inheritance of plastid characters in *Hosta japonica* Ashers. et Graebn. f. *albomarginata* Mak. and its derivatives. Cytologia 1: 192-215.

Dictionary of Dietetics. Rhoda Ellis. Philosophical Library, Inc., New York. 1956. 152 pp. \$6.00.

The definitions, comments and notations in this dictionary are evidently directed to employees with limited technical training who work in dietary departments. Most of the terms defined are related to human pathological states, diets prescribed for these states, or the management of a hospital dietary service. The text is admirable in brevity, clarity and in the type chosen, although in some instances good English usage has been sacrificed to economy. The chemical terms sometimes miss the point of interest to biologists, for example, citrulline is defined as a yellow amorphous plant resin, but it is more familiar to dietitians as a member of the cycle by which amino acids are relieved of their nitrogen component in the liver. Occasionally they are highly technical and in a few cases, simply incorrect, for instance hydrolysis is defined as "the chemical breakdown of a compound to another compound and water." In defining such diseases as diarrhoea, the treatment described is necessarily sketchy and of doubtful value to an uninformed reader.

The dictionary should serve a useful purpose in acquainting non-professional hospital employees with many of the strange medical terms involved daily in the work of a dietary department.

INEZ PRUDENT

Chemical Engineering Kinetics. J. M. Smith. McGraw-Hill Book Company, Inc., New York. First Edition, 1956. ix+402 pp. \$8.00.

This book deals with the engineering problems encountered in the design and operation of large scale reactors. It presupposes a knowledge of the elements of heat and mass transfer processes and some background in chemical thermodynamics. The underlying theory and the necessary technical tools are presented in the early chapters. These are followed by a discussion of reactor design beginning with the construction features and general design principles of several types of reactors each of which is then discussed in detail. New advances in interpreting catalytic reactions, particularly those occurring on solid catalysts are summarized and the important problem of diffusion in pores of solid catalysts is treated in a simplified, detailed fashion.

The book is well suited as a text for the fourth year of undergraduate work or for the first year of graduate work. The practicing engineer will also find it a convenient reference to the basic principles of reactor design. The inclusion of numerical illustrative examples throughout the book adds greatly to the clarity and understanding of the text.

WEBSTER B. KAY

NEMOBIUS MELODIUS, A NEW SPECIES OF CRICKET FROM OHIO

(ORTHOPTERA, GRYLLIDAE)

EDWARD S. THOMAS AND RICHARD D. ALEXANDER

Ohio State Museum, Columbus 10, and Department of Zoology and Entomology,
The Ohio State University, Columbus 10

The distinctive song of this cricket attracted the attention of the senior author in 1954. We were unable to secure specimens at that time, but the junior author secured tape recordings of the song. In 1956, we returned to the locality and secured specimens, and studies of the song were made in the laboratory by the junior author.

A search through The Ohio State Museum's series of *Nemobius carolinus*, with which the new form could easily be confused, resulted in the finding of a single female taken at Cincinnati, Ohio, in 1929. The junior author then discovered that tape recordings of a cricket song made at Cranberry Island, Licking County, Ohio, in September, 1954, and August, 1955, were indistinguishable from those of the new species; and specimens collected on those occasions proved referable to it.

Nemobius melodius n. sp.

This species is closely related to *Nemobius carolinus carolinus* Scudder and virtually indistinguishable from the latter in coloration and general structure. The females may be distinguished at a glance by their much longer ovipositor, and the males by the much larger number of teeth on the file of the stridulatory vein. The new species averages larger than *carolinus*, and all of our specimens are as intensively colored as the darkest individuals of *carolinus*. The song is distinctive, not closely resembling that of any other cricket known to us, and bearing little resemblance to that of *carolinus*.

Holotype. Male, taken in Carroll County, Ohio, Augusta Township, Section 34, 15 September 1956 (Edward S. Thomas and Richard D. Alexander). Form, coloration, and general appearance as in *Nemobius carolinus*, except for larger size and distinctiveness of file on stridulatory vein. Concealed genitalia as in *carolinus*. Measurements (in millimeters, made with ocular micrometer in binocular microscope): width of head, 2.46; width of pronotum, 2.52; length of pronotum, 1.86; length of body, 9.8; length of right tegmen (somewhat curled in mounting), 6.19; length of femur, 6.50; length of stridulatory vein from above, from inside edge of marginal vein to inside edge of ulnar, 1.39; number of teeth of file, 123.

Allotype. Female, same data. Same form and coloration as in *carolinus*, except for larger size and longer ovipositor. Coloration intensive. Measurements: width of head, 2.39; width of pronotum, 2.65; length of pronotum, 1.72; length of body, 9.94; length of right tegmen, 4.20; length of femur, 6.50; length of ovipositor, from caudal margin of dorsal projection at base to tip, 5.40.

Paratypes. 1 male, 7 females, same data; 1 male, Licking County, Ohio, Union Township, Cranberry Island, 15 September 1954, Richard D. Alexander; 1 male, 1 female, same locality, 21 August 1955, Richard D. Alexander; 2 females, same locality, 10 September 1954, Robert E. Woodruff; 1 female, Cincinnati, Ohio, 13 October 1929, Edward S. Thomas. All of our specimens are micropterous. The type series is in The Ohio State Museum. Paratypes will be deposited in The United States National Museum and The University of Michigan Museum of Zoology.

In addition to these, microscope slides were made of the right tegmina of 3 males of *melodius* from the type locality. These are included in the measurements in Table 1 for length of stridulatory vein and number of teeth only. The specimens are in alcohol and are not included in the paratypic series.

Individuals of the type series are quite constant in their relatively large size and their intensive coloration as compared with *carolinus*. As indicated in table 1, there is considerable overlap in measurements of *melodius* and *carolinus* in every character examined except the number and location of the teeth on the stridulatory vein and the length of the ovipositor. Nevertheless, in almost every character studied, the larger specimens of *melodius* fall outside the range of variation in *carolinus* and the smaller specimens of *carolinus* fall outside the range of *melodius*.

TABLE 1

A comparison of measurements of Nemobius carolinus and N. melodius

Morphological Character	Sex	<i>Carolinus</i>		<i>Melodius</i> (4♂, 13♀)
		Hebard (1915) (77♂, 101♀)	Ohio (10♂, 10♀)	
Width of head	♂	—	1.66-2.12	2.00-2.46
	♀	—	1.72-2.26	2.12-2.48
Caudal width of pronotum	♂	2.1-2.9	2.12-2.60	2.12-2.65
	♀	2.0-2.7	1.93-2.65	2.39-2.92
Length of pronotum	♂	1.6-2.0	1.13-1.61	1.53-1.86
	♀	1.6-2.0	1.30-1.80	1.66-1.95
Length of body	♂	6.9-8.8	6.38-8.82	7.75-9.80
	♀	6.3-8.4	6.60-8.85	8.25-9.94
Length of right tegmen	♂	4.8-5.8	4.13-5.80	5.25-6.19
	♀	2.9-4.4	2.57-4.00	3.32-4.20
Length of caudal femur	♂	5.5-6.4	4.25-5.75	5.40-6.50
	♀	5.0-6.4	4.32-6.25	5.85-6.90
Length of ovipositor	♀	2.6-3.9	2.59-3.10	4.69-5.40
Length of stridulatory vein	♂	—	0.86-1.06	0.98-1.39
Number of teeth on stridulatory vein	♂	—	(14 specimens) 51-63	(7 specimens) 110-125

There is a wide gap between the number of teeth of the stridulatory file in the specimens of the two species examined, those of *carolinus* ranging from 51 to 63, as compared with 110 to 125 in *melodius*. In addition, the extent of the file on the stridulatory vein differs considerably in the two forms. In *carolinus* the teeth of the file fall far short of the ulnar vein, while in our specimens of *melodius* the teeth extend beyond the ulnar vein (fig. 1). This character provides ready separation of the males of the two species without resorting to an actual count of the number of teeth.

There is also a wide gap in the measurements of the ovipositor in the specimens of the two species before us, the longest ovipositor of *carolinus* measuring 3.10 mm., the shortest of *melodius*, 4.69.

We have examined descriptions of the following forms considered to be synonyms of *carolinus* and find that the measurements given for ovipositor length are all considerably less than those of *melodius*: *volaticus* Scudder, 1877, 3 mm.; *septentrionalis* Provancher, 1877, 3.05 mm.; *affinis* Beutenmuller, 1894, 3-4 mm.; *exiguus* Blatchley, 1900, 3.5 mm.; *angusticollis* Walker, 1904, 3.3 mm.; *macdunnoughi* Urquhart, 1938, 3.1 mm.

The wide range of variation in *N. carolinus* in size and coloration, its wide ecological amplitude and certain differences in the song suggest the possibility that the form as now known may represent a complex, such as has been found in *Acheta*, *Anaxipha*, and the *Nemobius fasciatus* group (Fulton, 1931, 1952, 1956).

Song. The song of *melodius* is a smooth, clear, musical, high-pitched, continuous trill, in which the individual sound pulses are perceptible but far too rapid to count. The quality is somewhat reminiscent of the notes of an *Anaxipha*. It was the pleasing character of the song which suggested the name for the species. The contrast with the buzzing song of *carolinus* is so great that one would not suspect the close relationship of the two species.

Audiospectrographic analysis of the calling song of six individuals of *melodius* shows it to be a monorhythmic succession of sound pulses at rates varying from 24 to 39 per second at temperatures ranging between 65° and 80° F. Over this same range, the dominant frequency varied from 4.8 to 6.1 kilocycles per second. The calling song of 22 individuals of *carolinus* from Ohio,

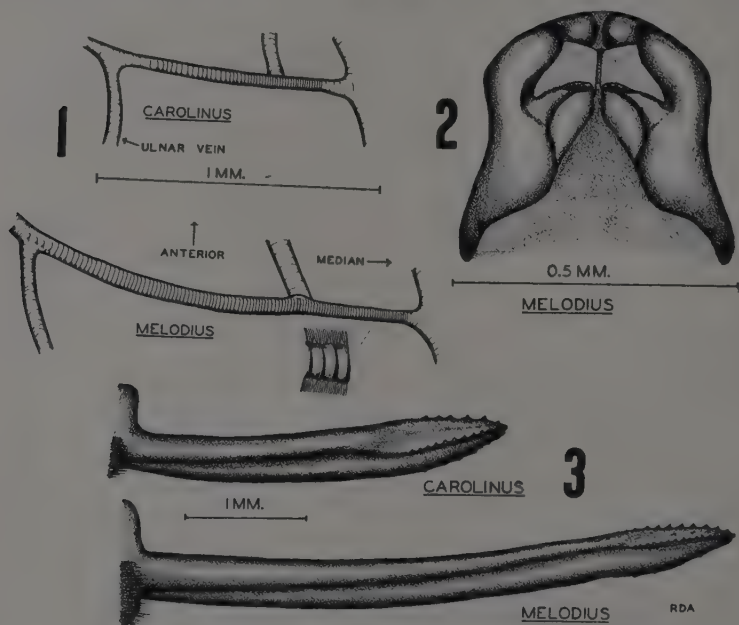


FIGURE 1. Ventral view of the stridulatory vein on the right tegmen of *Nemobius carolinus* and *N. melodius* (drawn from slides).

FIGURE 2. Ventral view of the male genitalia of *Nemobius melodius* (holotype).

FIGURE 3. Lateral view of the ovipositors of *Nemobius carolinus* and *N. melodius* (latter drawn from specimen No. 4, Carroll Co. O.).

Illinois, and Virginia varied from 58 to 76 pulses per second, and from 4.6 to 5.95 kilocycles per second over about the same temperature range. A fuller analysis of the songs will be found in an accompanying paper by Alexander.

Ecology. The specimens from the type locality were found in an extensive marsh, for guidance to which we are indebted to Mr. Forest Buchanan, of Amsterdam, Ohio. The marsh occupies a preglacial valley in the unglaciated Allegheny Plateau which was deeply filled with silts when the outlet of the original stream system was blocked by an early glacier. The swamp contains a number of northern relict plants, such as Toothed Arrow-wood (*Viburnum recognitum*, until recently known universally as *V. dentatum*), Winterberry (*Ilex verticillata*), Smaller Forget-

me-not (*Myosotis laxa*) and Speckled Alder (*Alnus rugosa*, formerly known as *A. incana*). The habitat in which the colony of *melodius* was found was, however, not unusual. The insects occurred at the margin of a portion of the marsh which was grazed by livestock, with scattered saplings of Pin Oak (*Quercus palustris*) and Cockspur Thorn (*Crataegus crus-galli*) and tangles of Swamp Rose (*Rosa palustris*). The wetter portions were densely vegetated with Soft Rush (*Juncus effusus*), Rice Cut-grass (*Leersia oryzoides*), Silky Cornel (*Cornus obliqua*), Arrow-leaf Tearthumb (*Polygonum sagittatum*), Sneezeweed (*Helenium autumnale*), Pinkweed (*Polygonum pennsylvanicum*), Broad-fruited Bur-reed (*Sparganium eurycarpum*) and several species of sedges. Technical names of plants are those of Gray's Manual of Botany, Eighth Edition.

The majority of our specimens of *melodius* were secured by tearing apart a soggy, decayed log, honey-combed with insect burrows, about 20 feet from the marsh proper. A number of individuals, however, were heard singing and some were collected in tussocks of marsh vegetation in the wetter portions. *Nemobius carolinus* was everywhere found associated with the new species. *Nemobius socius* swarmed in grassy places. Two specimens of *Tetrix subulata* Linnaeus a northern relict species, were collected in the area.

On the taller marsh vegetation, *Chorthippus longicornis* Latreille, *Melanoplus femur-rubrum femur-rubrum* DeGeer and *Oecanthus nigricornis* F. Walker were abundant. Other noteworthy species included *Orchelimum campestre* Blatchley, *Conocephalus nigropleurum* Bruner, and *C. attenuatus* Scudder.

Cranberry Island is a typical sphagnum-cranberry bog in Buckeye Lake. The colony of *melodius* was found in the sphagnum moss in the shrub border at the margin of the bog-meadow. *Nemobius carolinus* and *N. socius* were found abundantly in association with it.

It will be noted that the two foregoing stations have definite northern aspects. Such is not the case with the Cincinnati specimen. It was taken in the flood-plain of the Little Miami River. There are no northern relict bogs within many miles of this locality and, indeed, no sizeable marsh. The possibility exists, of course, that the specimen is mislabelled or that it was a waif, transported down stream on flotsam from farther north. This, however, must be purely speculative until careful field work throws more light on the ecology and distribution of the species.

N. melodius is apparently neither abundant nor wide-spread in distribution. The majority of the individuals at the type locality occupied a very small area, perhaps 10 yards square, with two or three singing males within a diameter of a hundred feet. The Cranberry Island colony was even more restricted. After a lapse of two and one years, respectively, the two colonies were found in the identical spots as on the previous visits. No other singing male was noted over large areas of similar habitat at either station.

Of 101 females of *carolinus* from Ontario, Pennsylvania, North Carolina, South Carolina, Georgia, and Texas, measured by Hebard in his monograph of the genus *Nemobius*, no specimen had an ovipositor measuring more than 3.9 mm. The large series of *carolinus* in The University of Michigan Museum of Zoology disclosed no female specimen with a long ovipositor.

The senior author has paid particular attention to the Orthopterous fauna of boreal relict bogs in Ohio for 29 years without having recognized the new species except at the type locality. However, in view of the fact that the males are unrecognizable in the field except by their song and the females scarcely more obvious, it is almost certain that the presence of the species has been overlooked in more than one locality. Careful field work in boreal relict bog situations in the northern United States and southern Canada should surely disclose additional stations for this interesting cricket.

ACKNOWLEDGMENT

The authors are indebted to Dr. Donald J. Borror of the Department of Zoology and Entomology, The Ohio State University, for critical examination of the manuscript. Thanks are also due to Dr. Theodore H. Hubbell, Director, and Dr. Thomas E. Moore, Curator of Insects, University of Michigan Museum of Zoology, for the privilege of examining the specimens of *Nemobius carolinus* at that institution, and for assistance in securing a copy of Provancher's description.

REFERENCES

- Alexander, R. D. 1957. The song relationships of four species of ground crickets (Orthoptera: Gryllidae: *Nemobius*). Ohio Jour. Sci. 57: 153-163.
- Beutenmuller, W. 1894. Notes on some species of North American Orthoptera, with descriptions of new species. Bull. Amer. Mus. Nat. Hist. 6: 249-252.
- Blatchley, W. S. 1900. On the species of *Nemobius* known to occur in Indiana. Psyche 9: 51-54.
- Fulton, B. B. 1931. A study of the genus *Nemobius* (Orthoptera: Gryllidae). Ann. Ent. Soc. Amer. 24: 205-237, 5 fig.
- . 1952. Speciation in the field cricket. Evolution 6(3): 283-295, 4 fig.
- . 1956. The genus *Anaxipha* in the United States (Orthoptera: Gryllidae). Jour. Elisha Mitchell Sci. Soc. 72(2): 222-243, 23 fig.
- Hebard, M. 1913. A revision of the species of the genus *Nemobius* (Orthoptera: Gryllidae) found in North America north of the Isthmus of Panama. Proc. Acad. Nat. Sci. Phila. 1913:394-492, 32 fig.
- Provancher, L. 1876. Petite Faune Entomologique du Canada. —Les Orthopteres. Nat. Can. 8(2): 52-62.
- . 1877. Petite Faune Entomologique du Canada et particulièrement de la Province de Quebec. —Les Orthopteres et les Neuropteres. pp. vi+157. Quebec.
- Scudder, S. H. 1877. New forms of saltatorial Orthoptera from the southern United States. Proc. Bost. Soc. Nat. Hist. 19: 35-41.
- Urquhart, F. A. 1938. A new species of *Nemobius* from Ontario (Orthoptera). Canad. Ent. 70: 101-102, 1 fig.
- Walker, E. M. 1904. The crickets of Ontario. Subfamily Gryllinae. Canad. Ent. 36: 181-188, 12 fig.

Journal of Molecular Spectroscopy. Harald H. Nielson, Ed. Academic Press, Inc., New York. 1957 Vol. I (four issues). \$10.00.

This journal will be devoted to publication of original research papers dealing with molecular spectra in emission and absorption, molecular spectra in the ultraviolet, the visible, the infrared, and the microwave regions. It will also include contributions on Raman, spectroscopy radio-frequency, and nuclear magnetic resonance spectroscopy.

The editor, of the Department of Physics, The Ohio State University, will be assisted by an Editorial Advisory Board representing leading spectroscopy laboratories in several parts of the world.

F. W. F.

Unit Operations of Chemical Engineering. Warren L. McCabe and Julian C. Smith. McGraw-Hill Book Company, Inc., New York. First Edition, 1956. ix+945 pp. \$10.50.

This book is intended as an introductory text to acquaint the beginning engineer and technologist with the unit operations of chemical engineering. Fifteen of the major unit operations are discussed separately and in such detail that the student will have no difficulty in proceeding to the more advanced chemical engineering texts.

The text is well illustrated. Numerous diagrammatic sketches of equipment and charts of engineering data are given. The inclusion of the numerical solutions to many illustrative problems and the list of problems to be solved by the student at the end of each chapter, add greatly to the value of the book as a teaching text.

WEBSTER B. KAY

THE SONG RELATIONSHIPS OF FOUR SPECIES OF GROUND CRICKETS

(ORTHOPTERA: GRILLIDAE: *NEMOBIUS*)¹

RICHARD D. ALEXANDER

Department of Zoology and Entomology, The Ohio State University, Columbus 10

INTRODUCTION

Several accounts have been written of the mating behavior of different species of ground crickets (Fulton, 1931; Richards, 1952; Gabbutt, 1954), and many excellent descriptions of their songs, based on auditory impressions, have appeared (Fulton, 1930, 1931, 1932; Cantrall, 1943; and many others). A few song analyses have been made with mechanical or electronic devices (Fulton, 1933; Pielemeier, 1946, 1946a; Pierce, 1948). Detailed comparative studies of song relationships in the singing Orthoptera and Cicadidae are almost non-existent, though it is increasingly apparent that satisfactory interpretations of the taxonomic and distributional relationships of these species will depend on such studies.

The present investigation is based on laboratory and field observations, and on tape recordings of songs analyzed by means of a Vibralyzer. The species discussed include *Nemobius carolinus carolinus* Scudder, *N. confusus* Blatchley, and *N. melodius* Thomas and Alexander, the only eastern representatives of the subgenus *Eunemobius* Hebard. A fourth species, *N. maculatus* Blatchley, belonging in the subgenus *Allonemobius* Hebard, is also considered here because of certain distributional and song relationships with the above species.

The recordings used for song analysis are deposited in the Library of Animal Sounds, Department of Zoology and Entomology, The Ohio State University. They were made with a Magnemite, Model 610-E (in the field) and a Magnecoorder, Model PT6A (in the laboratory) at a tape speed of fifteen inches per second. American Microphone Company Microphones, Models D-33 and D-33A, were used, both in the field and in the laboratory. Explanations of the Vibralyzer and its uses can be found in Borror and Reese (1953) or Alexander (1956, 1957).

Crickets in the genus *Nemobius*, as well as other ground-inhabiting crickets in general, produce the calling song both day and night, though usually more individuals in a colony are involved in song at any particular time at night than at any time during the day. None of the ground crickets are known to synchronize or alternate the periodical elements of their songs as do species in several different genera and subfamilies of Tettigoniidae and Gryllidae which live on vegetation.

Aside from the calling song, many *Nemobius* species produce variously distinctive and complex sounds during courtship and during encounters between males. Apparently all *Nemobius* species possess some sort of female-attracting gland, in American species at the base of the spine on the hind tibiae, and in European species on the right tegmen (Fulton, 1931; Richards, 1952, 1953). Some species have not been heard to produce sounds during courtship, and in others there is only intermittent sound production at wide intervals, such as occurs in most of the tree crickets (Oecanthinae) which possess a highly developed metanotal gland. In *Nemobius* species as well as other crickets, jiggling and jerking of the

¹This study has been supported by grants from The Ohio State University Development Fund, the Graduate School of The Ohio State University, and the Rockefeller Foundation. The author is indebted to Dr. Edward S. Thomas of the Ohio State Museum and Dr. Donald J. Borror of the Department of Zoology and Entomology of The Ohio State University for advice and assistance.

body during the various stages of courtship, in time with the courtship song if one is produced, suggests that rhythm sometimes operates as a visual stimulus in courtship.

Key to the Calling Songs of Species Compared Here
(Based on characteristics apparent to human ears)

1. More or less continuous trills, or rapid successions of sound pulses, usually lasting several minutes without perceptible breaks. 2
- 1'. A rhythmic succession of short trills, 3-5 delivered in 5 seconds, each trill lasting $\frac{1}{2}$ to 1 second, beginning softly and increasing in intensity, then ending abruptly. Sometimes short, detached portions occur before or after each trill, or the first part of the trill is rather jerky or pulsating. *Nemobius confusus* Blatchley
- 2(1). A smooth, clear (musical), high-pitched, continuous trill in which the individual sound pulses (each caused by a single wingstroke) are perceptible, but far too rapid to count. *Nemobius melodius* Thomas and Alexander
- 2'. Jerky or pulsating trills, rarely smooth, and in such cases the individual sound pulses are delivered so rapidly that they are individually completely imperceptible and a buzzing or droning effect is created. 3
- 3(2'). A jerky trill in which the catches occur regularly at about 3-8 per second (depending on temperature). *Nemobius maculatus* Blatchley
- 3'. A buzzing or droning trill which may take one of the following three forms; (a) a pulsating trill in which rapid pulsations are delivered at 10-13 per second (rare), (b) a smooth trill completely lacking in pulsations perceptible to the ear (rare), or (c) a trill which consists of an alternation of (a) and (b) at a rate of 1-3 cycles in two seconds, and with the intensity reduced during the smooth phase of the cycle (most common of the three forms). *Nemobius carolinus* Scudder

Nemobius melodius Thomas and Alexander²

The Melodious Ground Cricket

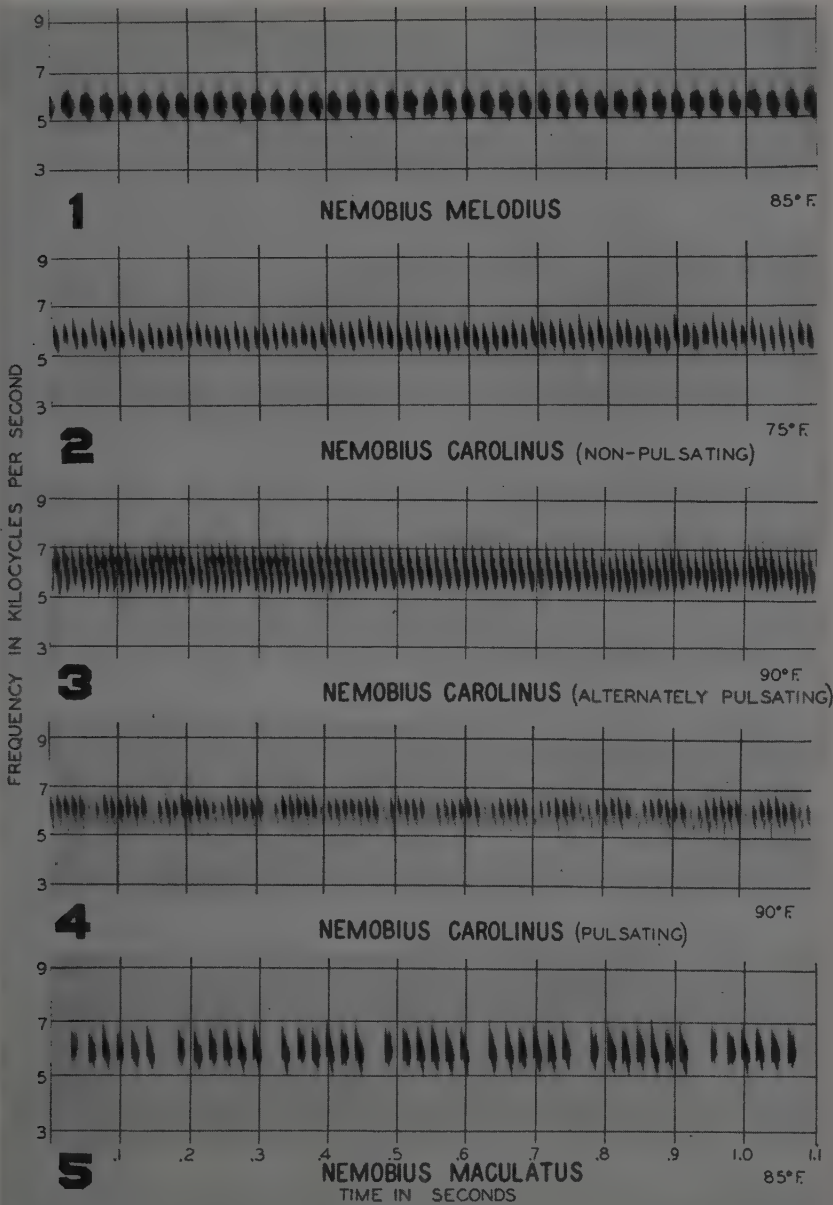
The songs of six individuals of this species have been recorded, four from Licking County, Ohio (two in the laboratory and two in the field), and two from Carroll County, Ohio (one in the laboratory and one in the field). A total of 25 minutes and 42 seconds of the calling song was recorded. A male caged with several females was recorded for 4 minutes and 38 seconds, and during this time he produced 12 brief bursts of song (fig. 6) which resemble closely a short trill that males of *carolinus* produce around females, and which is probably associated with courtship. This short trill is also structurally similar to the individual trills in the calling song of *confusus* (fig. 7 to 9). This type of song relationship—the calling song of one species being similar to the courtship song of a closely related species—also occurs between *N. fasciatus* (DeGeer) and *N. tinnulus* Fulton. The short trills of *carolinus* and *melodius* are the only courtship sounds noticed in any of the species discussed here, and their simplicity and infrequent production indicates that their function in courtship is probably slight.

The calling song of *melodius* is compared to those of *carolinus* and *maculatus* in figures 1 to 5. When undisturbed, an individual producing the calling song strokes the tegmina fairly continuously and evenly, often for several minutes at a time. However, when disturbed, or when changing position (this latter some-

²The songs of this species were erroneously attributed to *N. palustris* Blatchley and to "*Anaxipha?* undescribed" by Alexander (1956) (pp. 146-148; 204-205; figs. 89, 94, 111).

EXPLANATION OF FIGURES IN PLATE I

1. Calling song of *N. melodius*.
2. Non-pulsating calling song of *N. carolinus*.
3. About one cycle of the alternately pulsating calling song of *N. carolinus*.
4. Pulsating calling song of *N. carolinus*.
5. Calling song of *N. maculatus*.



times occurs frequently), a singing male introduces almost imperceptible breaks into his song, sometimes involving the deletion of only one or two pulses. In addition, he may slow the rate of tegminal motion, at the same time lowering the intensity of the sound slightly. These traits are also characteristic of the songs of *carolinus* and *confusus* and serve as recognition characters for the songs of species in the subgenus *Eunemobius*. In both *carolinus* and *confusus*, however, these fluctuations in intensity and pulse rate have become rhythmical elements in the song. In *melodius* they occur at irregular intervals, and without any consistent pattern.

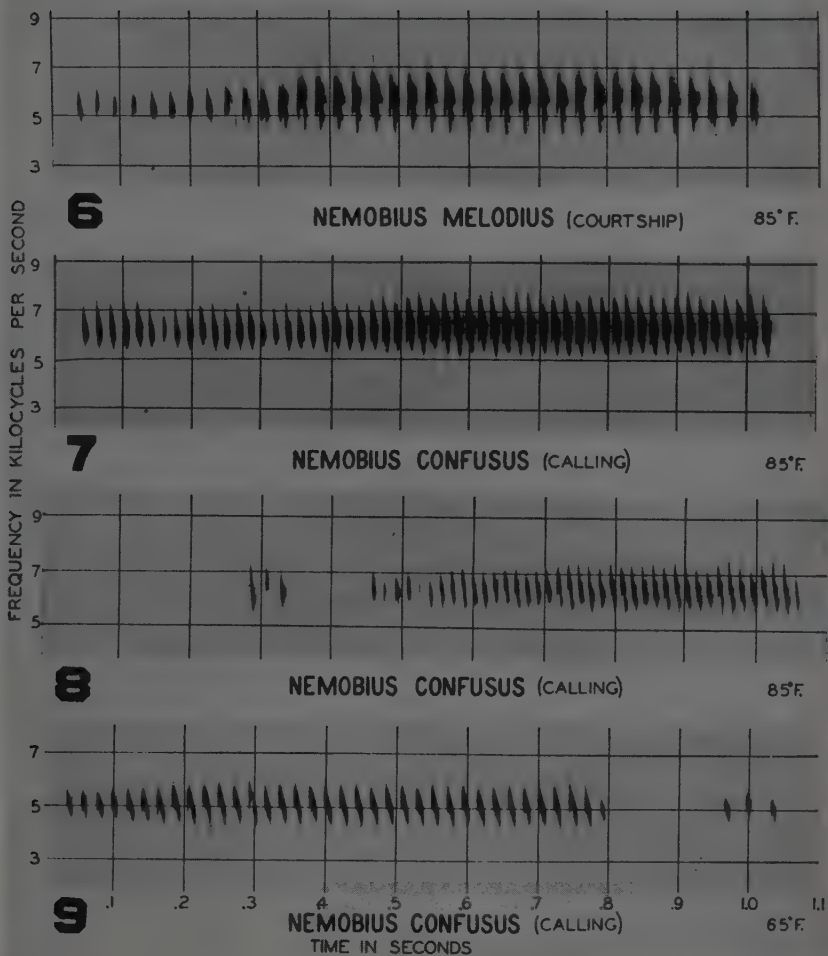
As shown in figure 10, the calling songs of *carolinus* and *melodius* differ considerably in pulse rate at the same temperature and frequency. Each symbol in the diagram represents the song of a different individual, analyzed from audiospectrographs of one second or more of the song. The frequency determinations are averages of five readings made from section Vibragrams (intensity versus frequency) of the same second of song. A comparison of recordings of one individual each of the two species from Carroll County, Ohio, made at 78 and 79° F, respectively, shows that the songs are pitched at about 5.6 and 5.8 kilocycles per second. However, the song of *melodius* at this temperature has a wingstroke rate producing 34 pulses per second, while *carolinus* produces 75 pulses per second.

The dominant frequency in cricket songs has usually been considered to correspond to the number of teeth on the stridulatory vein or file that are struck per second (Lutz and Hicks, 1930; Alexander, 1956). Thus, a difference in pulse rate can either be due to a difference in the actual speed of motion of the tegmina (distance travelled per unit time), to a difference in the length of the stroke, or to a combination of these factors. In the first case there should also be a difference in the frequency caused by the rate of file toothstrike, providing the file teeth are spaced the same in both species; in the second case the toothstrike rate would be the same in the two species.

It is difficult to make an exact comparison of the teeth per unit space on the file since this varies, the teeth being progressively more widely spaced toward the lateral end of the file (fig. 1, Thomas and Alexander, 1957). This differential spacing is probably reflected in the downslurring in frequency which can be detected in each pulse in cricket songs. This downslurring might also be attributed to a drop in speed of motion of the tegmina during file-scraper contact. However, when brief contact of the file and scraper occurs on the "backstroke" (probably the opening of the tegmina), a slight rise in frequency occurs, indicating that file-tooth spacing is probably the important factor.

Due to the downslurring of each sound pulse and the differential spacing of the file teeth (and since we do not know exactly what portion of the file is involved in sound production), it is difficult to make an exact correlation between frequency and file spacing. However, by expanding audiospectrographs timewise, counts can be made of the number of teeth struck during each sound pulse. Such counts in several pulses of the songs of two specimens recorded from Carroll County, Ohio, at 78 and 79° F, showed that *carolinus* used 25-33 file teeth per sound pulse, while *melodius* used 57-73. This difference indicates that the pulse rate differences between the songs of the two species chiefly involves a difference in the length of the stroke of the tegmina rather than in the actual speed of their motion. The difference in number of teeth struck per sound pulse is correlated with the actual number of teeth in the file which ranged from 51 to 63, in 14 individuals of *carolinus*, and 110 to 127, in 7 individuals of *melodius*.

A number of morphologically ill-defined species have been revealed in the singing Orthoptera (Fulton, 1931, 1952, 1956; Alexander, 1956, and unpublished data) which have song differences of varying degree. It is often assumed that these song differences should be reflected in differences in the external sound-



EXPLANATION OF FIGURES IN PLATE II

6. Presumed courtship trill of *N. melodius*.
7, 8, and 9. Single trills from the calling song of *N. confusus*.

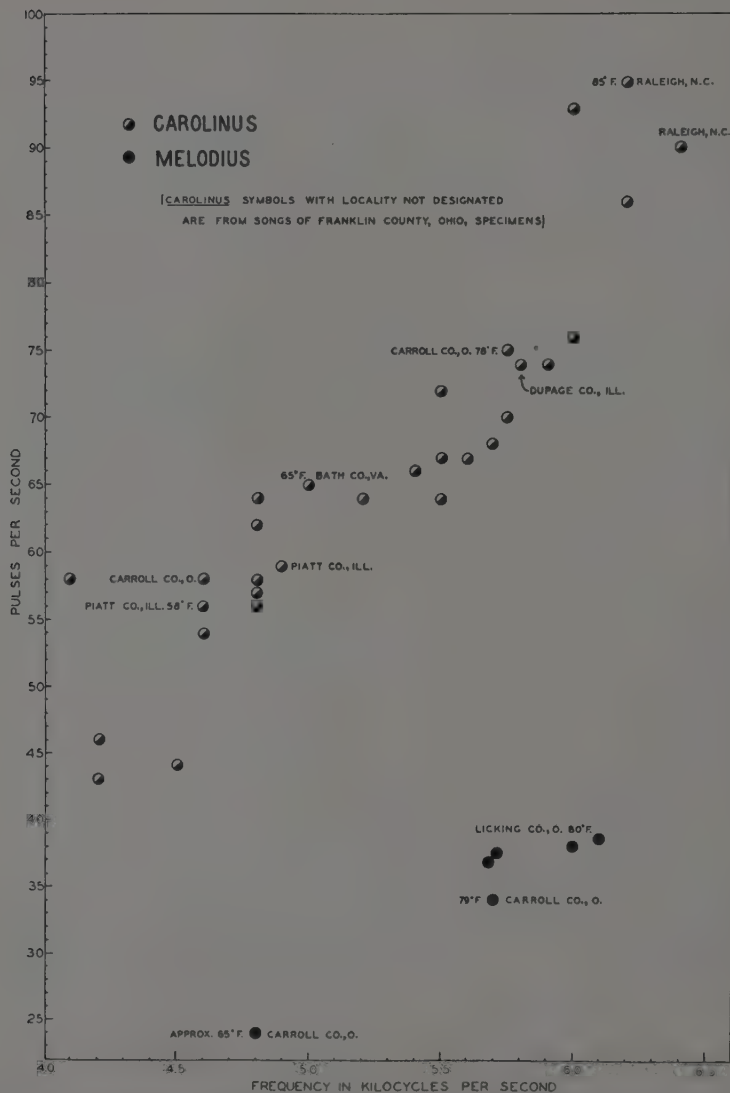


FIGURE 10. A comparison of pulse rate and frequency in the calling songs of *Nemobius carolinus* and *N. melodus* recorded at different places and at different temperatures.

producing structures. In such cases, however, the song differences are chiefly or entirely differences in rhythm. The length of the file and the spacing of its teeth are probably the only characters in which taxonomists can expect to find differences correlated with differences in the song rhythms of closely related species. In most cases, rhythm differences do not involve the external sound-producing structures in any way.

Nemobius carolinus Scudder

The Carolina Ground Cricket

Twenty-nine individuals of this species were recorded from the localities indicated in figure 10, for a total of 11 minutes and 5 seconds of the calling song.

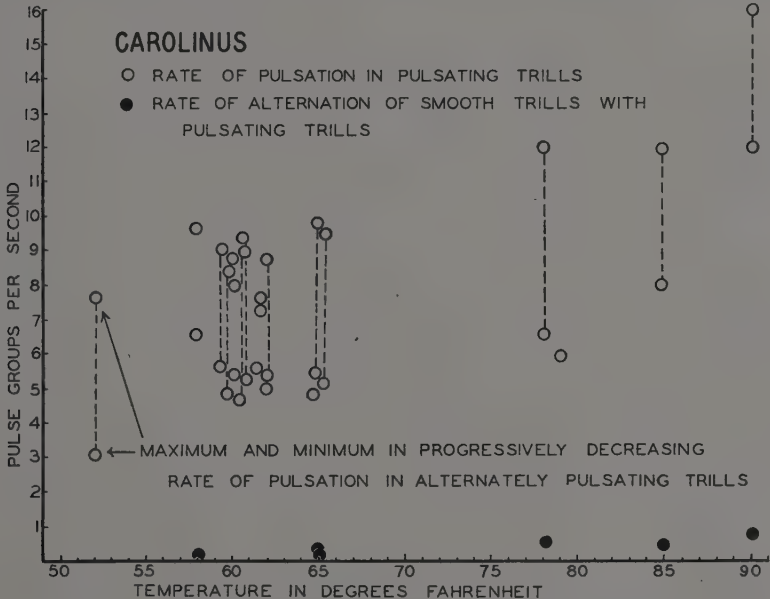


FIGURE 11. The rates of delivery of rhythmical elements superimposed on the basic pulse rate in the calling songs of *Nemobius carolinus* recorded at different temperatures.

The short trills produced around females and probably connected with courtship were heard on several occasions both in the laboratory and in the field, but no recordings were obtained.

The calling song of *carolinus* is a continuous trill resembling that of *melodius* in the characteristics mentioned above. However, considerable variation occurs in the recorded songs attributed to this species, with respect to the presence or absence and regularity of changes in intensity and pulse rate (see key above). The most commonly heard song involves an alternation of two types of trills, one smooth and the other pulsating as a result of every 6th to 8th pulse being de-emphasized (fig. 3). The complexity of this song is further increased by a progressive decrease in the rate of pulsation (progressive increase in the number of pulses between de-emphasized pulses) during each pulsating phase or cycle. Progressive changes of this sort occur frequently in the more complicated insect songs, and

are often quite consistent, suggesting possible behavioral significance. In addition to the alternately pulsating type of trill, some individuals always damp every sixth or seventh pulse (fig. 4), and others trill evenly all the time (fig. 2). These variations cannot be correlated with geographic locality or habitat, and the two extremes may occur in the songs of individuals collected only a few feet apart. A few of the recordings are of individuals which have imperfectly or irregularly pulsating songs that may be intermediates. No differences in pulse rate or

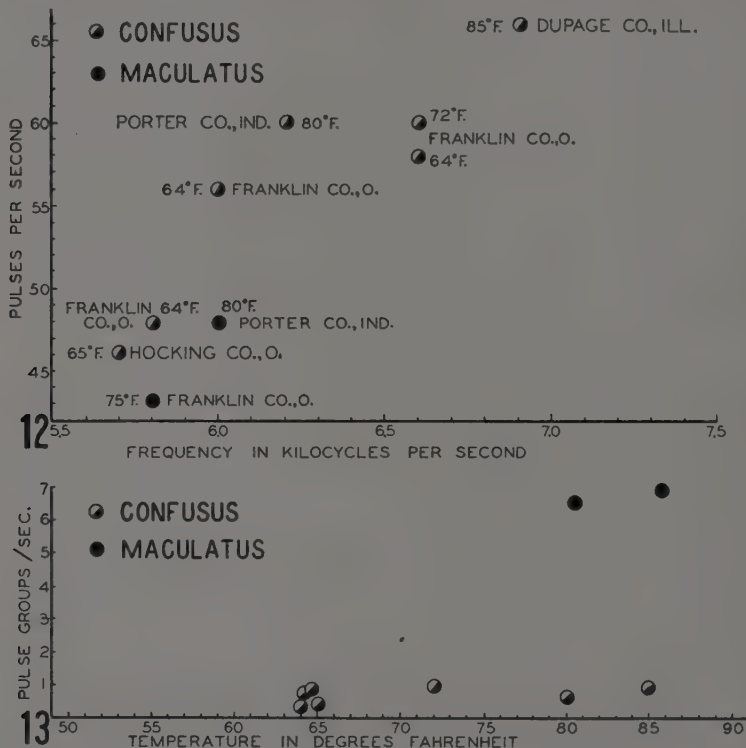


FIGURE 12. A comparison of pulse rate and frequency in the calling songs of *Nemobius confusus* and *N. maculatus* recorded at different places and at different temperatures.

FIGURE 13. The rates of delivery of pulse groups in the calling songs of *Nemobius confusus* and *N. maculatus* recorded at different temperatures.

frequency have been found between the three types of song, and it seems likely that this is intraspecific variation, and that it is of genetic origin rather than associated with variations in the stimulus situation.

As shown in figure 10, the pulse rate in the songs of all individuals recorded varies from 43 to 95 per second, and the frequency varies from 4.2 to 6.4 kilocycles per second over a temperature range of about 50 to 90° F. Figure 11 shows that the rate of pulsation due to the damping of occasional pulses is quite variable, and ranges from 3 to 16 per second. The rate of alternation of pulsating and non-pulsating cycles varies from 5 to 44 cycles per minute.

Cantrall (1943) gives a detailed description of the song of Michigan specimens which corresponds closely to that given above for the alternately pulsating trill. He says the complete cycles of pulsation and non-pulsation occur about 24 times a minute. Fulton (1931) gives the same description for specimens from Iowa and North Carolina, adding (p. 226), "Rarely males will be heard that seldom sing without beats, but usually there is a regular repetition of the two phases of the song, sometimes one second for each period and sometimes longer. Sometimes when starting to sing this species will sound a few notes which increase in volume and then die out." Pierce (1948, New Hampshire) obtained a frequency of 5430 cycles per second at 70 pulses per second from analysis of a pulsating song in which every 6th to 8th pulse was de-emphasized. These figures agree well with those obtained here.

Nemobius confusus Blatchley

The Confused Ground Cricket

Seven individuals of this species were recorded, from the localities indicated in figure 12, for a total of 6 minutes and 24 seconds of the calling song. No other sound has been heard. The calling song consists of a succession of short trills, each lasting $\frac{1}{2}$ to 1 second and occurring at rates of 2-5 in 5 seconds. Each of the trills begins rather softly and increases gradually in intensity until it ends abruptly. Some individuals preface each trill with 1-4 short, soft pulsations (fig. 8), sometimes completely detached from the rest of the trill. Sometimes these detached portions seem to come after the trill rather than before it (fig. 9). The individual trills in this song, as mentioned above, closely resemble the short trills produced by *carolinus* and *melodius* during courtship (cf. fig. 6 and 7). This song is also more closely related to the calling song of *carolinus* than would seem in a superficial comparison. If the intervals between trills were cut out, the result would be a more or less continuous trill similar in structure to the alternately pulsating trill of *carolinus*. In the song of one specimen of *confusus*, there are places where the trills are run together, causing it to sound very much like *carolinus*.

As shown in figure 12, the pulse rate in the calling song of *confusus* varies from 46 to 66 per second, and the frequency varies from 5.7 to 6.9 kilocycles per second between 64 and 85° F. In ten trills analyzed, there were from 36 to 56 pulses per trill.

This song has apparently been described only by Fulton (1931, 1932) who observed specimens which attached 2 and 3 of the brief pulsations to the front of the trill. He gives trill rates as follows: Iowa, 70° F, 1-2 per second; Raleigh, North Carolina, 75° F, 9-10 per 10 seconds, and 80° F, 10-13 per 10 seconds.

Nemobius maculatus Blatchley

The Spotted Ground Cricket

Two individuals of this species were recorded from the localities indicated in figure 12, for a total of 3 minutes and 40 seconds of the calling song. No other sound was noticed in cultures containing both males and females.

The calling song is a rather soft, continuous trill with a regular "skip" occurring at a rate of about 6.8 per second at 85° F. As shown in figure 5, this skip is a slight gap after every 6th or 7th pulse, as if one pulse had been left out. The pulse rate within pulse groups was 43 and 48 per second in the two specimens recorded, and the frequency of the two songs was 5.8 and 6.0 kilocycles per second, respectively (fig. 12).

The pulsating trill of *carolinus* bears an interesting relationship to this song, since it has every 6th to 8th pulse de-emphasized, or softer than the others. If the beat caused by this damping of every 6th to 8th pulse is behaviorally significant,

one can easily imagine an accentuation of this character by the complete loss of this pulse. It would be interesting to know if *maculatus* strokes its tegmina silently during the skip in its song, or holds or slows them momentarily. *N. maculatus* and *carolinus* are not closely related, and it is unlikely that the song of one is derived from a song immediately ancestral to the other. However, comparison of the songs of *carolinus*, *maculatus*, and *confusus* illustrates two possible methods of transition from a trilling or continuous monorhythmic song to a dirhythmic chirping song (very short pulse groups produced at long intervals, such as in *Acheta*).

The song of *maculatus* has been described by Fulton (1931) who says that in the song of an Iowa specimen the beat occurred 36 times in 10 seconds at 61° F, and 6 times per second at 70° F.

DISCUSSION

Taxonomists have long been aware of the high degree of consistency in the calling songs of the different individuals of a given species of Orthoptera, and the noticeable differences which almost invariably occur between the songs of different species. New species have been detected and are still being detected by differences in their songs that are a great deal more obvious, even to the ear alone, than are their morphological peculiarities. The song relationships demonstrated here indicate that detailed song comparisons may also be of value in clarifying phylogenetic relationships. The songs of *carolinus*, *confusus*, and *melodius*, though strikingly different in many individual elements of rhythm, still contain similarities which indicate mutual relationship, and which set them apart from the song of *maculatus*, a species placed in another subgenus on the basis of morphological characters.

Comparison of the types of song differences existing among the four species and the frequency with which the species occur mixed together in the same colonies in the field, indicates that variations in certain rhythmical elements may be more closely correlated with ecological distribution than with phylogenetic relationship. Thus, the basic pulse rate in the song of *melodius* is more different from that in the song of *carolinus* than it is from those in the songs of the other two species. The basic pulse rate is the only rhythmical element in the song of *melodius*, and although *carolinus* is the closest known relative of *melodius*, it is also the only *Nemobius* species found together with it in the field, other than *socius* which has a completely different song. *N. confusus* and *maculatus*, species which frequently live together and belong in different subgenera, have basic pulse rates much closer to that in the song of *melodius* than does *carolinus*, and even closer to each other. However, the songs of these species contain an additional rhythmical element, the rate of delivery of pulse groups, which is superimposed on the basic pulse rate. In this character they differ greatly. If this type of correlation is generally true, it would seem to substantiate the view that certain interspecific song differences are behaviorally significant, and operate as species-isolating mechanisms.

Comparisons of the individual elements of rhythm in the song of *carolinus* with those in the songs of *maculatus* and *confusus* are more difficult because of the complicated nature of this song, and particularly because of the introduction of progressive changes in intensity and in the length of pulse groups. The trills of *confusus* are delivered at a rate near the rate of alternation of smooth trills with pulsating trills in the alternately pulsating trill of *carolinus*, but *confusus* has no song characteristic resembling the rate of delivery of pulse groups in the pulsating trill of *carolinus*. Likewise, though the rate of delivery of pulse groups in the song of *maculatus* is near that which occurs in the song of *carolinus*, *maculatus* has no song character corresponding to the rate of alternation of pulsating and smooth trills in the alternately pulsating song of *carolinus*.

REFERENCES

- Alexander, R. D. 1956. A comparative study of sound production in insects, with special reference to the singing Orthoptera and Cicadidae of the eastern United States. xviii+529 pp., 180 fig. (Unpublished Ph.D. Dissertation, The Ohio State University).
- . 1957. Sound production and associated behavior in insects. *Ohio Jour. Sci.* 57: 101-113, 13 fig.
- Borror, D. J. and C. R. Reese. 1953. The analysis of bird songs by means of a Vibralyzer. *Wilson Bull.* 65(4): 271-275, 7 fig.
- Cantrall, I. J. 1943. Orthoptera and Dermaptera of the George Reserve, Michigan. *Mich. Mus. Zool., Univ. Mich. Misc. Publ.* 54: 1-182, 3 fig., 2 maps, 15 tab., 10 pl.
- Fulton, B. B. 1930. A new species of *Nemobius* from North Carolina (Orthoptera: Gryllidae). *Ent. News* 41: 38-42, 1 fig.
- . 1931. A study of the genus *Nemobius* (Orthoptera: Gryllidae). *Ann. Ent. Soc. Amer.* 24: 205-237, 5 fig.
- . 1932. North Carolina's singing Orthoptera. *Jour. Elisha Mitchell Sci. Soc.* 47: 55-69.
- . 1933. Inheritance of song in hybrids of two subspecies of *Nemobius fasciatus* (Orthoptera). *Ann. Ent. Soc. Amer.* 26: 368-376, 1 fig.
- . 1952. Speciation in the field cricket. *Evolution* 6(3): 283-295, 4 fig.
- . 1956. The genus *Anaxipha* in the United States (Orthoptera; Gryllidae). *Jour. Elisha Mitchell Sci. Soc.* 72(2): 222-243, 23 fig.
- Gabbutt, P. D. 1954. Notes on the mating behavior of *Nemobius sylvestris* (Bosc.) (Orth., Gryllidae). *Brit. Jour. Animal Behavior* 2(3): 84-88, 5 fig.
- Lutz, F. E. and W. R. Hicks. 1930. An analysis by movietone of a cricket's chirp (*Gryllus assimilis*). *Amer. Mus. Novit.* No. 420: 1-14, 2 tab., 5 fig.
- Pielemeier, W. H. 1946. Supersonic insects. *Jour. Acoust. Soc. Amer.* 17: 337-338.
- . 1946a. Seeing summer sounds. *Sci. Month.* 62: 450-452.
- Pierce, G. W. 1948. The Songs of Insects; with related material on the production, propagation, detection, and measurement of sonic and supersonic vibrations. Cambridge, Mass., Harvard Univ. Press. vi+329 pp., 243 fig., 26 tab.
- Richards, T. J. 1952. *Nemobius sylvestris* in S. E. Devon. *Entomologist* 85: 83-87; 108-111; 136-141; 161-166.
- . 1953. *Nemobius sylvestris* (F.) (Orthopt., Gryllidae): a correction and some further notes. *Entomologist* 86: 133-134.
- Thomas, E. S. and R. D. Alexander. 1957. *Nemobius melodioides*, a new species of cricket from Ohio. *Ohio Jour. Sci.* 57: 148-152.

A Textbook of Entomology. H. H. Ross. John Wiley & Sons, Inc., New York. Second edition-1956. xii+519 pp. \$7.75.

The second edition of Dr. Ross' fine textbook presents under one cover a composite introduction to entomology suitable for use by students of biology, and for general reference by the layman as well as the scientist.

The book begins with an excellent account of the growth of entomology in North America, an often neglected aspect. Following there is a chapter devoted to arthropods related to insects, and four well illustrated chapters giving a thorough discussion of the external and internal anatomy, physiology and embryology, and life cycle of insects. The orders and families of insects are reviewed in enough detail to give a general understanding and a background of information. Illustrated keys to the commoner families are included. The final three chapters present detailed accounts of insect geological history and evolution, and the principles of ecology and insect control.

The reviewer feels that the revised addition improves the features of the original and is a creditable contribution to scientific textbook writing.

EDWARD N. LAMBREONT

ANNUAL REPORTS OF PROCEEDINGS AND SPECIAL PAPERS

1892—1931

ANNUAL REPORTS

First to Fortieth (except 11th and 18th)	\$1.00 each
Set of First to Fortieth (except 11th and 18th)	\$30.00

SPECIAL PAPERS

1. Sandusky Flora. pp. 167. E. L. Moseley	\$1.00
2. The Odonata of Ohio. pp. 116. David S. Kellicott	2.00
3. The Preglacial Drainage of Ohio. pp. 75. W. G. Tight, J. A. Bownocker, J. H. Todd and Gerard Fowke	1.00
4. Tabanidae of Ohio. pp. 63. James S. Hine	1.00
5. The Ecological Study of Big Spring Prairie. pp. 96. Thomas A. Bonser75
6. The Coccidae of Ohio. I. pp. 66. James G. Sanders	1.00
7. Batrachians and Reptiles of Ohio. pp. 54. Max Morse	1.50
8. Ecological Study of Brush Lake. pp. 20. J. H. Schaffner, Otto E. Jennings, Fred J. Tyler75
9. The Willows of Ohio. pp. 60. Robert F. Griggs75
10. Land and Fresh-water Mollusca of Ohio. pp. 35. V. Sterki	1.00
11. Discomycetes in the Vicinity of Oxford. pp. 54. Freda M. Bachman75
12. The Pteridophytes of Ohio. pp. 41. John H. Schaffner	1.00
13. Fauna of the Maxville Limestone. pp. 65. W. C. Morse75
14. The Agaricaceae of Ohio. pp. 116. W. G. Stover	2.00
15. An Ecological Study of Buckeye Lake. pp. 138. Frederick Detmers	1.00
16. Flora of the Oak Openings West of Toledo. pp. 56. E. L. Moseley75
17. The Cedar Cliffs Prairie Opening of the Cincinnati Region. pp. 36. N. Mildred Irwin75
18. Milk Sickness Caused by White Snakeroot. pp. 171. E. L. Moseley75

Please make checks payable to The Ohio Academy of Science. Residents of Ohio please include sales tax.

Address: GIFT AND EXCHANGE LIBRARIAN
The Ohio State University, Columbus 10, Ohio.

Progress In Nuclear Energy. Biological Sciences Series Six. Volume I. *J. C. Bugher, J. Coursaget, and J. F. Loutit*, Editors. McGraw-Hill Book Co., Inc., New York. Pergamon Press Ltd., London. 1956. 205 pp. \$7.00

This volume deals with the uses of radioisotopes and other forms of nuclear energy in the biological sciences. Most of the material presented here is a series of reviews of already published material. However, the writers, the reviewers, and the editors all appear to be leaders and pioneers in applying nuclear energy to biological problems; consequently the information is quite useful.

One important function this book serves is to bring to the attention of biologists some of the kinds of problems that can be approached and solved with radioisotopes. More important than this perhaps, is that here one can become acquainted with a variety of useful techniques in handling and using radioisotopes and in evaluating results of research.

It would seem that Chapter 8, which is the last and deals with "The Use of Radioisotopes in Biochemistry" is too brief, being only five pages in length. This seems to be an extremely short presentation for so important a phase of biological research.

WILLARD C. MYSER

THE STRUCTURE OF FOREST SOILS¹

WILLARD H. CARMEAN

*Athens Forest Research Center,
Central States Forest Experiment Station,
Athens, Ohio*

How soil particles are arranged in forest soil directly influences the growth of forest trees. This arrangement of particles and their size and shape, or "structure" of the soil, affect soil porosity and hence aeration. Soil porosity is important to the growth and development of tree roots because it affects the diffusion of oxygen to tree roots and the diffusion of excessive concentrations of carbon dioxide from areas adjacent to tree roots (Kramer, 1949). Coile (1948), in studies of the growth and productivity of stands of loblolly and shortleaf pine, concluded that the site quality of trees is generally determined by soil depth and by physical soil factors that influence moisture availability and aeration.

Soil structure determines the number, size, and continuity of soil pores and is important to both forest and agricultural land because it is related to the quantity, quality, and periodicity of water yield. Studies by Bayer (1948) and by Nelson and Bayer (1940) have shown the percolation rate of water through soil is largely related to the quantity of large pores in the soil. When there are few large pores, water percolates slowly through the soil. If more rain falls than the soil can absorb, surface water runoff will occur, often causing erosion, sedimentation, and floods.

Numerous studies of water infiltration, water runoff, and sedimentation have shown that water percolates into forest soils faster than it does in agricultural or abandoned agricultural soils (Auten, 1933; Dils, 1953; Hoover, 1950; Colman, 1953; Lutz and Chandler, 1947). Studies by Auten (1933, 1941) in Ohio and in the Central States Region show that forest stands have infiltration rates from 50 to 700 times those of adjacent abandoned old fields. Harrold (1953, 1954) found that a wooded watershed at Coshocton, Ohio had less surface runoff than nearby grassland or cropland watersheds. Dils (1953) studied the effects of mountain farming at Coweeta, North Carolina, and reported that marked increases in water runoff, siltation, and stream peak flow resulted from converting a steep mountain forest watershed to corn and pasture. Rothacher (1953), reporting on the effects of reforestation and the elimination of fire and grazing on the White Hollow watershed in eastern Tennessee, found that these practices had reduced summer peak stream flows 73 to 92 percent and that runoff caused by summer storms was reduced as much as 500 percent without any decrease in the total annual stream flow.

Comparing soil characteristics and land-use methods for forest and agricultural land may help in understanding the reasons for the deteriorated soil

¹Paper presented before Conservation Section, Ohio Academy of Science, Athens, Ohio, April 16, 1954.

Structure is an important characteristic of forest soil because it affects both tree growth and water yield. Numerous tree-site-quality studies have indicated that the most productive forest land has deep, medium-textured soils that are loose and well aerated. Studies of both forest and agricultural soils have shown that more water infiltrates and less runs off soils with such structure.

In this paper, general forest and agricultural soil conditions are compared to show the differences in soil structure that result from different cultural treatments and vegetational covers. In general, undisturbed forest soils have better structure than soils that are used for agriculture. The superior structure of forest soil is one of the major reasons for the superior quality and periodicity of water yields from forested watersheds. Reforesting abandoned or submarginal land is urged as a means to improve the water relations of such land.

structure and the poor water yield from some agricultural land. Such a comparison may explain the objectives of many of the conservation practices that are directed toward improving soil structure and increasing movement of water into and through the soil.

Land Use

Forest land is usually land that is too poor, too rough, or too inaccessible to be farmed profitably. In most parts of eastern United States the better land has been cleared for agriculture while the poorer land has been left in forest, or if cleared, has been abandoned and left to return to forest cover. Agricultural land is usually devoted to crops that are harvested annually while forest crops are harvested only at long intervals. The high value of agricultural crops warrants intensive cultural practices, whereas the comparatively low value of the infrequently harvested forest crop warrants less intensive care. On forest areas land management involves cuttings that may include harvest cuts and occasional interim silvicultural treatments.

Soil Properties of Forest and Agricultural Land

A forest soil is a natural or only slightly disturbed material that took centuries to develop under permanent forest cover. A succession of genetic soil layers is present, ranging from the very important surface organic layers down to the mineral parent material. The continual depositing of tree litter upon the ground for many decades has developed the characteristic surface layers of organic matter found in forest areas. Relatively little organic matter is lost by the infrequent and incomplete harvesting done on forest land. The organic matter on the surface and in the lower layers is maintained by relatively slow oxidation resulting from cool, shaded microclimatic conditions and from the lack of the disturbing effects of cultivation used on agricultural land.

On most agricultural land the surface organic layers and surface soil horizons have been mixed and altered beyond identity by decades of cultivation. Large amounts of organic matter and nutrients are annually lost when crops are harvested. Furthermore, the incorporated organic matter decomposes more rapidly because cultivation and high temperatures help speed up oxidation.

When forests are removed and the land is used for agriculture, the soil structure generally deteriorates. This deterioration, evidenced by reduced pore space, increased bulk density, increased compaction, reduced content of water-stable aggregates, and reduced rates of infiltration, has marked effects on surface water runoff, stream flow, and sedimentation.

The structure of forest soils is developed and maintained by many factors of the forest environment. The soil surface is protected from the impact of raindrops because the forest canopy and surface organic layers absorb the energy of falling raindrops. Unprotected agricultural soil, however, is frequently exposed to the direct beating action of raindrops with the result that soil aggregates are shattered and dispersed. Soil colloids are suspended and are washed into and deposited in the larger pores that are necessary for the rapid infiltration and percolation of water.

Organic matter on and in forest soil helps improve and maintain soil structure (Lutz and Chandler, 1947). Organic colloids and materials synthesized by soil fungi and bacteria are important in the formation of soil aggregates (Stallings, 1952). Soils used for agriculture, however, do not usually have enough organic matter in the surface layers to maintain the large populations of microorganisms found in forest soils. Reduced action of microorganisms as well as reduced organic colloid content is thus partially related to the poor structure of many agricultural soils.

In addition to microorganisms a forest soil has a relatively high population of macroorganisms that favors soil structure and produces many large burrows and channels (Lutz and Chandler, 1947). Gaiser (1951, 1952) studied the distribution of tree roots in the soil beneath white oak stands of southeastern Ohio and found that the surface soils had a very high concentration of small roots and that the vertical channels formed by larger roots in the surface and subsoil exceeded 4,000 per acre. The large number of root channels, as well as the excellent structure of forest soils, undoubtedly accounts for the rapid infiltration rates and reduced runoff of surface water so often reported from forest land.

Cultivating agricultural land that is too wet frequently produces cloddy or puddled conditions that cause a decrease in aggregation and porosity (Baver, 1948). Plowing and other forms of tillage may actually crush soil aggregates and thus reduce porosity. Heavy machinery may compact the surface layer of soil. Excessive grazing of both agricultural and forest soil usually compacts the surface soil layers and causes increased water runoff because of decreased soil porosity and water infiltration rates (Auten, 1933; Johnson, 1952).

AGRICULTURAL VS. FOREST SOILS

Agricultural Soil

DEEP productive soils on level or gently sloping land. Land used for annual crops of high value. Cultivation, fertilization, and land-conservation practices frequently used.

DISTURBED soils whose surface, organic layers have lost their identity through cultivation.

INCORPORATED ORGANIC CONTENT USUALLY LOW because of decreased litter deposition, annual crop removal, and increased oxidation resulting from cultivation and increased solar insolation.

SLOWER RATES of water infiltration and percolation than forest soil due to a decreased content of large pores.

POORER STRUCTURE than forest soil because of lower content of organic matter, decreased activity of macro and microorganisms, exposure to raindrop action, washing of soil colloids into soil pores, increased erosion, mechanical effect of cultivation and grazing that crush soil aggregates and compact surface soil layers.

Forest Soil

SHALLOW, less productive soils on steep or poorly drained land. Land used for forests with long intervals between harvests. Limited cultural practices include harvest cuts and occasional interim silvicultural treatments.

NATURAL soils with undisturbed organic layers and soil horizons.

INCORPORATED ORGANIC CONTENT HIGH because of continual deposition of forest litter, long intervals between harvest, and lower rates of oxidation.

FASTER RATES of water infiltration and percolation than agricultural soils because of the surface organic layers, large numbers of root channels extending into subsoil, and a high content of large soil pores.

BETTER STRUCTURE than agricultural soil because of higher content of organic matter, large numbers of macro and microorganisms that form channels and promote aggregate formation, protection from raindrop action, relatively little washing of soil colloids into soil pores, and large numbers of roots in surface and subsoil layers.

CONCLUSIONS

Most of the land presently used for agriculture in the eastern United States was once occupied by forests; in Ohio, for example, the forest cover has been reduced from an estimated 95 percent to 21 percent. This conversion of land to agricultural use has been necessary for the settlement and development of our country; but, it has frequently caused soils to deteriorate. Change in soil structure,

reduced water infiltration, rapid water runoff, erratic stream flow, and downstream flooding and sedimentation are symptoms of the deterioration of much of this land that has been converted from forest to farms.

Soil conservation practices are being successfully applied on many agricultural lands. These practices help to improve soil structure, soil stability, soil hydrologic characteristics, and water yields. Practices such as mulching, crop rotation, terracing, contouring, and strip farming have been remarkably successful in correcting many of the major soil problems of agricultural land.

Many problems still exist, however, especially on hilly land and land marginal for farming. Large land areas in Ohio and eastern United States have been, are now, and will be abandoned and will eventually revert to forest. Much land, now being grazed or cultivated, is considered too poor to warrant spending time or money for the needed conservation practices. This land is responsible for many of the water problems of Ohio and eastern United States. Reclaiming and improving this land should be a major consideration in watershed programs designed to rectify the unfavorable stream conditions of many river basins.

Reforestation is advocated on land not suitable for farming as a means of making non-productive land productive of valuable forest crops. Converting this land to forest cover will improve soil structure, increase water infiltration, and reduce water runoff and erosion.

LITERATURE CITED

- Auten, J. T.** 1933. Porosity and water absorption of forest soils. *Jour. Agr. Res.* 46: 997-1014, illus.
- . 1941. Forest soil properties associated with continuous oak, old-field pine, and abandoned field cover in Vinton County, Ohio. *Cent. States Forest Expt. Sta. Tech. Note* 34. 8 pp.
- Baver, L. D.** 1948. *Soil Physics*. 2nd Ed. 398 pp. John Wiley and Sons, Inc., New York.
- Coile, T. S.** 1948. Relation of soil characteristics to site index of loblolly and shortleaf pines in the lower Piedmont region of North Carolina. *Duke Univ. School of Forestry Bul.* 13. 78 pp.
- Colman, E. A.** 1953. *Vegetation and Watershed Management*. 412 pp. The Ronald Press Co., New York.
- Dils, R. E.** 1953. Influence of forest cutting and mountain farming on some vegetation, surface soil, and surface runoff characteristics. *Southeast. Forest Expt. Sta. Sta. Paper* 24. 55 pp.
- Gaiser, R. N., and J. R. Campbell.** 1951. The concentration of roots in the white oak forests of southeastern Ohio. *Cent. States Forest Expt. Sta. Tech. Paper* 120. 13 pp., illus.
- . 1952. Root channels and roots in forest soils. *Soil Sci. Soc. Amer. Proc.* 16: 62-65, illus.
- Harrold, L. L.** 1953. Water and land management. Paper delivered before Ohio Forestry Assoc., Columbus, Ohio Jan. 22, 1953. 15 pp.
- . 1954. Relation of plant cover and land use to water intake and ground water. *Proc. of the Third Annual Ohio Water Clinic*. Ohio State Univ. Coll. of Engin. Spec. Report. pp. 90-96.
- Hoover, M. D.** 1950. Hydrologic characteristics of South Carolina Piedmont forest soils. *Soil Sci. Soc. Amer. Proc.* 14: 353-358.
- Johnson, E. A.** 1952. Effect of farm woodland grazing on watershed values in the southern Appalachian mountains. *Jour. Forestry* 50: 109-113, illus.
- Kramer, P. J.** 1949. *Plant and Soil Water Relationships*. 347 pp. McGraw-Hill Book Co., Inc., New York.
- Lutz, Harold J., and R. F. Chandler Jr.** 1947. *Forest Soils*. 514 pp. John Wiley and Sons, Inc., New York.
- Nelson, W. R., and L. D. Baver.** 1940. Movement of water through soils in relation to the nature of the pores. *Soil Sci. Soc. Amer. Proc.* 5: 69-76.
- Rothacher, J. S.** 1953. White Hollow watershed management: 15 years of progress in character of forest, runoff, and streamflow. *Jour. Forestry* 51: 731-738, illus.
- Stallings, J. H.** 1952. Soil aggregate formation. *U. S. Dept. Agr., Soil Conserv. Serv.* TP-110. 23 pp.

CONTRIBUTIONS TO THE HISTORY OF *HYDRASTIS CANADENSIS* (GOLDENSEAL) IN OHIO

ANNA H. KOFFLER, PH.D. AND MILAN G. GORBY, JR.

*Department of Pharmacognosy, College of Pharmacy,
Ohio Northern University, Ada, Ohio*

Goldenseal is a plant indigenous to Ohio, Indiana, Kentucky and West Virginia. Cincinnati, Ohio was so very close to the geographical center of the supply that it soon became the first commercial center for this drug. In 1793, The Transactions of the American Philosophical Society published a paper by Hugh Martin read before this society under the title "An Account of Some of the Principle Dyes Employed by the North American Indians." The author referred to the roots of *Hydrastis canadensis*, stating that it might well be called "radix flava Americana." In 1798, B. S. Barton called the attention of the medical world to the medicinal use of *Hydrastis canadensis* by the Cherokee Indians. One such use against inflammation of the eye is reported by Captain Lewis from the Lewis and Clark expedition. Lewis wrote (1815):

Having procured sufficient quantity of the roots, wash them clean and dry them in the shade, break the roots as fine as possible with the fingers, place them in a glass vessel about two-thirds full, add rain or river water until vessel is filled, shaking it frequently, and it will be fit for use in the course of six hours. The water must be decanted, that remaining with the root is to be frequently applied by wetting a piece of linen and touching the eye gently with it.

Rafinesque in his Medical flora of 1828 devoted much space to the drug. In 1833, the editor of the Thomsonian Recorder, added it to the Thomsonian Materia Medica. In the same year Wooster Beach included it in his work "The American practice of medicine." The author was the founder of the American reformed school of medicine which later merged with the eclectic school. The above mentioned book was the standard work of the new movement and was recognized all over the world. The drug *Hydrastis* did not appear in the first edition of the United States Dispensatory, also published in 1833. The second edition in 1834 gave it a slighting reference which was carried through unchanged for the next ten years. The Eclectic Dispensatory by King and Newton in 1852 made the drug conspicuous; thereafter, it was much used and it was included in the Pharmacopeia of the United States in 1860.

During this entire period and up through 1870, Goldenseal was quite abundant in Ohio. The price ranged from eight to twelve cents per pound. In 1884, John Uri Lloyd wrote:

Only a small area of the country can yield the drug in amount sufficient to repay collection at present prices, and of this section of country but a limited portion actually contributes any of it to the market. It does not necessarily follow, however, that the plant will not disappear in sections, where it now grows abundantly, but which have never yielded the drug to commerce. *Hydrastis* is so sensitive to climatic influence that even a partial destruction of the timber causes it to shrink away and one turn of the soil by the plow blots it from existence. If it were like *Podophyllum*, content to thrive in woodland pasture, the future would be brighter; as it is, each year witnesses a shrinkage in area and a loss to the world of this peculiarly interesting American plant. *Hydrastis* has nearly vanished from the rich hillsides bordering the Ohio river and is no longer found in the populous sections of our valley.

Twenty-eight years later Dr. Lloyd made an even stronger plea (1912a). "If it is proper to preserve a lingering group of bison, or to search the land over for our vanishing wild pigeon," he wrote, "why is it not proper to conserve, with the help of the strong hand of authority, America's valued flora from absolute extermination?"

As is the case with other articles of trade, prices begin to rise as shortages become acute. The price of *Hydrastis* had been from eight to twelve cents a

pound. In the next twenty years the price rose to fifty-five cents per pound; by 1904 it rose to \$1.00; and in the next year to \$1.50 per pound. In the next seven years still higher prices were obtained, up to \$4.00 per pound. The peak prices were reached in the years 1917 and 1918, when the crude drug brought 5 to 6 dollars per pound; and the price for a pound of the powdered drug ranged from \$6.50 to \$6.75.

One hardly wonders that the following protest was published in one of the first copies of the Journal of the American Pharmaceutical Association (Dohme and Englehardt, 1912):

We cannot refrain from expressing the hope that something be done to eliminate the largely used drug Golden Seal from the itching palms of the money lenders, because it can truly be said of this drug that it is in the hands of a trust and an unscrupulous one at that. To think of being compelled to pay four dollars and more a pound for a wild and freely growing plant indigineous to this country when it can easily and profitably be raised for less than one dollar a pound, only accentuates the fact that the Sherman Bill (Sherman Anti-trust Act, 1890. Authors' note) may even be made applicable to crude products of nature.

Since the drug brought such fabulous prices, much substitution and adulteration by other roots and rhizomes took place. The fame of *Hydrastis*, however, grew and it was included in the Pharmacopeias of many countries. Early in the twentieth century a survey was made by a number of physicians, none of whom belonged to the Eclectic School. All were graduates of colleges of professional standing. The survey dealt with the comparative value of many medicinal plants. The roots and rhizomes of *Hydrastis canadensis* ranked fifteenth in importance and were chosen by 36 physicians. Right above the roots and rhizomes of *Hydrastis canadensis* ranked the leaves of *Digitalis purpurea*; the dried ripe seed of *Nux vomica* took twelfth place receiving five votes. (Lloyd, 1912b).

In another survey, which included all the vegetable drugs included in the Pharmacopeia of the United States, 1900, *Hydrastis* did even better. This vegetable drug ranked second in importance receiving 5634 votes. More than ten thousand physicians had participated this time. All again were graduates of recognized colleges. The first place went to a write-in, an unofficial plant, the Night-blooming *Cereus* (*Cactus Grandiflorus*). The vegetable drugs Aconite, Gelsemium and Ipecac followed *Hydrastis* receiving 5,618, 5,540, and 5,501 votes respectively. The surprising fact was that the exclusively American drug plant, *Hydrastis canadensis* took precedence over *Aconitum napellus*. Aconite, representing the dried tuberous roots of the latter plant, was the great favorite among physicians of all schools of medicine at that time. (Lloyd, 1912b).

Hydrastis is still a favorite with many. It has been included in the latest, the tenth edition of the National Formulary which was published in 1955.

REFERENCES

- Barton, B. S. 1789-1804. Collections Toward a Materia Medica of the United States. Philadelphia.
- Beach, W. 1833. American Practice of Medicine. New York.
- Dohme, A. R. L., and H. Englehardt. 1912. Drug quality during the period 1905 to 1911. Jour. Amer. Pharm. Assoc. 1: 99-103.
- Lewis, M., and W. Clarke. 1815. Travels to the Source of the Missouri River and across the American Continent in 1805-6. London.
- Lloyd, J. U. 1884-85. Drugs and Medicines of North America. Cincinnati, Ohio.
- . 1912a. The cultivation of *Hydrastis*. Jour. Amer. Pharm. Assoc. 1: 5-12.
- . 1912b. Vegetable drugs employed by American physicians. Jour. Amer. Pharm. Assoc. 1: 1228-41.
- Martin, H. 1793. Account of the principal dyes employed by the North American Indians. Trans. Amer. Phil. Soc.
- The National Formulary. 1955. Tenth Ed. Amer. Pharm. Assoc., Washington, D. C.
- Rafinesque, C. S. 1828-30. Medical Flora or Medical Botany of the U. S., Philadelphia.
- Thomsonian Recorder. 1832-1837. Columbus, Ohio.

TAXONOMY OF THE GENUS *HELIOPSIS* (COMPOSITAE)¹

T. RICHARD FISHER

Department of Botany and Plant Pathology, The Ohio State University, Columbus 10

The genus *Heliopsis* is a member of the tribe Heliantheae of the family Compositae. It is represented by thirteen species, all of which are restricted to the western hemisphere. Although some of the species, particularly those of the United States, have received attention recently, there has been a great deal of confusion with regard to the status of several taxa. This confusion, in part, has been due to the lack of study of the genus throughout its entire range.

The genus is separated from other genera of the tribe in possessing fertile disk flowers, as well as fertile, persistent ray flowers, with marcescent ligules, achenes void of a pappus, or pappus of a slight crown of one or two short chaffy awns.

In order to gain information concerning relationships the problem was attacked in three ways: by a study of herbarium specimens,² by studying as many collections as possible in the research garden, and by studying populations in nature. These techniques involved conducting a hybridization program, cytological study, and an investigation of the ecological conditions throughout the range of the species.

History

In 1753, Linnaeus described species now referred to *Heliopsis* under the following three genera: *Bupthalamum*, *Silphium*, and *Rudbeckia*. *Bupthalamum helianthoides* was described from material collected in Pennsylvania, North Carolina, and Virginia, whereas *Silphium solidaginoides* and *Rudbeckia oppositifolia* were described from material from Virginia. These errors persisted until 1807 when Persoon described the genus *Heliopsis* and placed the three Linnaean species in synonymy. However, Persoon did not retain the earliest specific epithet employed by Linnaeus. Instead, he named the smooth-leaved taxon *Heliopsis laevis*. In 1826, R. Sweet recognized that *Bupthalamum helianthoides* L. and *Heliopsis laevis* Pers. were the same taxon. Consequently, he restored the Linnaean epithet of *helianthoides* in the publication, "Hortus Britannicus." Sweet's treatment unfortunately, was not generally known to the authors of American Floras until the late 1800's, thus the specific epithet employed by Persoon persisted for some time for the widely distributed *H. helianthoides* (L.) Sweet.

In his account of *Heliopsis* for the "Prodromus" of DeCandolle, (1836), Cassini treated the genus in three sections and recognized six species, two of which had been proposed by Hooker (1835) in "Companion to the Botanical Magazine." The sections were separated on the basis of achene characteristics and the number of series of involucre bracts.

In 1835, Rafinesque described the genus *Heliopsis*, as then known, under the generic name of *Helepis*. Three species, *H. grandifolia*, from the Carolinas, *H. parviflora* and *H. angustifolia* from eastern Kentucky, were included in this genus. The species were separated on the basis of leaf shape and achene characteristics.

Torrey and Gray in "Flora of North America" (1842) accepted *H. laevis* Pers. as the only valid species and reduced *H. scabra* Dun. and *H. gracilis* Nutt. to varieties. Gray's later treatment of the North American flora (1878), reinstated

¹Publication 606, Department of Botany and Plant Pathology, The Ohio State University.

²In order to conserve space, citation of specimens has been eliminated. A duplicated list of specimens examined and cited for this study is being sent to the major herbaria of the United States. The reader is also referred to the microfilm reproduction of the author's Ph.D. thesis on file at the University of Michigan library.

H. scabra and *H. gracilis* as species and added *H. parvifolia*, a newly described taxon from the southwestern United States and northern Mexico. In addition to the four taxa in the United States, he included a Mexican species, *H. buphthalmoides* Dun.

In 1797, Jacques described *Heliopsis buphthalmoides* under the genus *Anthemis*. From his description it is difficult to determine his reasons for this, except that in *Anthemis*, the rays may be fertile or neutral, and may be yellow, but are more often white. The type specimen has not been examined, but in *Anthemis* the leaves are alternate and pinnately dissected, a condition which never exists in *Heliopsis*. In 1819, Dunal transferred the species to *Heliopsis*, but failed to give Jacques credit for the specific epithet.

M. L. Fernald (1937) described *H. helianthoides* var. *solidaginoides* from herbarium material of this country as well as from the British Museum and the Linnaean Herbarium. He concluded that *Silphium solidaginoides* L. was a southern form of *H. helianthoides* (L.) Sweet.

A Summary of the Chronological History of the Genus:

1. Linnaeus, C. (1753) Sp. Pl. Stockholm. 2: 904.
2. Jacques, N. J. (1797) Hart. Schoenb. 2: 13.
3. Persoon, C. H. (1807) Syn. 2: 474.
4. Dunal (1819) Mem. Mus. Paris 5: 56.
5. Cassini, H. (1822) Dict. Sc. Nat. 24: 327.
6. Rafinesque, C. S. (1825) Neogynt. 3: 231.
7. Sweet, R. (1826) Hort. Brit. 487.
8. Hooker, J. D. (1835) Comp. Bot. Mag. 1: 98.
9. De Candolle, A. (1836) Prodr. 5: 551.
10. Torrey, J. & Gray, A. (1842) Fl. No. Amer. 2: 303.
11. Gray, A. (1878) Syn. Fl. No. Amer. 2: 254.
12. Fernald, M. L. (1937) Rhodora 39: 456.

General Morphology

Caudex and roots.—The species of *Heliopsis* are herbaceous and perennial with the exception of four annual species, which are endemic to Mexico.

The persisting structure of the perennials is a woody caudex with a mass of branched and unbranched fleshy roots. Growth in the spring is from lateral buds along the underground rhizome. The root system varies with the environmental conditions in which the plant grows. In the more moist mesophytic habitats of the midwestern and eastern United States, southern Mexico and Central America, a fibrous root system prevails, but in the more xerophytic areas of the southwestern United States a modified tap root develops. Neither the caudex nor the root furnishes any feature of taxonomic value in distinguishing species; and the fact that these structures are seldom collected renders them valueless when dealing with herbarium material.

Stem.—The characters of the stem, especially the upper portions, afford some means of separating species. Rough, hispid or scabrous pubescence is an important distinguishing character in the species of the United States. Other species are pilose, hirsute or villous. The indumentum is generally confined to the upper stems or lateral branches and leaves.

Leaves.—The leaves, which are always opposite, afford good criteria in separating species. Four taxa, *H. brachactis*, *H. parvifolia*, *H. rubra*, and *H. helianthoides* ssp. *occidentalis* exhibit a deltoid, or deltoid-ovate type of leaf shape (fig. 1). In *H. filifolia*, the leaf is filiform. In other species the leaf shape is lanceolate, ovate or ovate-lanceolate.

The petiole length is a valuable character in separating *H. helianthoides* ssp. *occidentalis* from *H. helianthoides* ssp. *helianthoides*, the petiole of the latter always

being 1.5 cm. or longer, and that of the former seldom attaining 1.5 cm. and more often being nearly sessile.

The leaf margins are most often irregularly dentate, but occasionally, in some species, they are nearly entire or merely irregularly crenulate. The texture is mostly leathery and quite firm, but in the annual species it is usually thin and papery.

Involucre.—The phyllaries are of little value in separating taxa since they are highly variable within a given species in regard to shape, size, and pubescence. The species of the United States usually possess foliaceous outer phyllaries, whereas the species of Mexico and South America possess phyllaries which are only occasionally foliar.

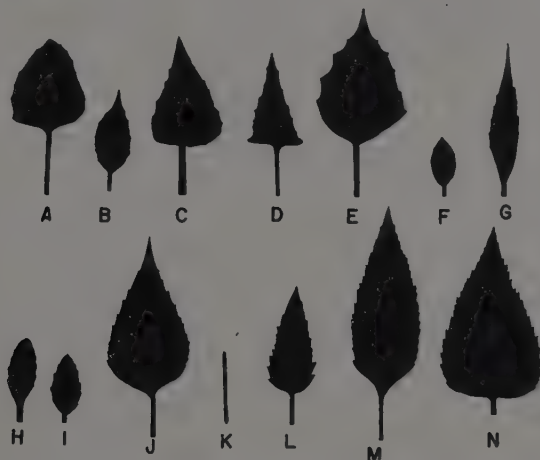


FIGURE 1. Leaf outline drawing of species of *Heliopsis*. A. *H. annua*; B. *H. parviceps*; C. *H. brachactis*; D. *H. parvifolia*; E. *H. rubra*; F. *H. procumbens*; G. *H. lanceolata*; H. *H. decumbens*; I. *H. longipes*; J. *H. bupththalmoides*; K. *H. filifolia*; L. *H. gracilis*; M. *H. helianthoides* ssp. *helianthoides*; N. *H. helianthoides* ssp. *occidentalis*. Reduced $\frac{3}{4}$ natural size).

Receptacle and palea.—The receptacle is broadly convex and hollow, although only inconspicuously so in *H. helianthoides*. The pales are lanceolate, acute, conduplicate, becoming stiff and persistent after maturity. The color of the apex is red, purple or yellowish-brown, and offers ready means of separating certain taxa.

Corollas.—The heads are heterogamous with styliferous, fertile ray flowers and perfect, fertile tubular disk flowers. The corollas of both the ray and disk flowers are yellow in all taxa except *H. brachactis* and *H. parviceps*, in which they are deep purple.

Pappus.—The genus is characterized by the absence of the pappus, although occasionally in the taxa of the United States, especially *H. helianthoides* ssp. *scabra*, the pappus is rarely represented by 2–3 chaffy awns or a crenulate ridge.

Geographic Distribution of the Genus

The known areas of distribution of *Heliopsis* are shown on the maps which accompany the taxonomic treatment. In general, herbarium material of the North American taxa has been ample to plot distributions with a great deal of

accuracy, but there are still some large disjunctions, particularly in the southern and southwestern areas of the United States and Mexico. Herbarium material examined from Central and South America is insufficient to plot accurate distributions of all taxa. In some instances only the holotype has been available for study. In others, the distribution seems to be disjunct for several reasons. As mentioned above, it may be due to the incompleteness of collections. On the other hand, the species may be rare and consequently seldom collected.

The plants included in this study occur in southern Canada, United States, Mexico, Central America and South America. In Canada, *Heliopsis* occurs only in the southern portions of Quebec, and westward to southeastern Saskatchewan. In the United States, the genus is widespread, ranging from Maine westward to North Dakota, southward through the Great Plains to New Mexico and eastward through eastern Texas to northern Florida.

From southeastern Arizona and southwestern Texas the genus ranges southward through Mexico, Central America and into South America to central Bolivia.

TABLE 1

Tabular arrangement of material which furnished cytological counts (In all, n=14)

<i>H. helianthoides</i> ssp. <i>helianthoides</i>	
Tippecanoe Co., Indiana	D. M. Smith s.n.
Monroe Co., Indiana	T. R. Fisher 533
Crawford Co., Indiana	C. B. Heiser, Jr. 3275
Cattaraugus Co., New York	C. B. Heiser, Jr. s.n.
Botetourt Co., Virginia	W. P. Stoutemire s.n.
Richland Co., Ohio	R. W. Long 528
<i>H. helianthoides</i> ssp. <i>occidentalis</i>	
Depage Co., Illinois	F. Swink s.n.
St. Louis Co., Minnesota	*O. Lakela s.n.
St. Croix Co., Wisconsin	C. B. Heiser, Jr. 3253
<i>H. helianthoides</i> ssp. <i>scabra</i>	
Shannon Co., Missouri	C. B. Heiser, Jr. (seedling transplant)
Franklin Co., Missouri	T. R. Fisher 410
Reynolds Co., Missouri	C. B. Heiser, Jr. (seedling transplant)
<i>H. parvifolia</i>	
U. S. D. A., Beltsville, Maryland**	
<i>H. annua</i>	
Guanajuata, Mexico	*L. A. Kenoyer 2412
<i>H. rubra</i>	
near Puerto Escondido, Baja California, Mexico	*A. Carter 2866

* Seed obtained from herbarium specimens.

** Exact location of source material unknown.

Cytology

Cooper and Mahony (1935) reported a chromosome number of $n=16$ in *H. helianthoides*. This number has never been found in this species or any other species examined during the course of this investigation. Instead, a chromosome number of $n=14$ has been found in *H. helianthoides* as well as in *H. annua*, *H. parvifolia* and *H. rubra*. In *H. helianthoides*, several collections from the mid-western and eastern United States were examined (table 1, fig. 2).

Meiotic division figures were regular in all material studied. Microsporocytes were smeared using the acetocarmine smear technique after preliminary fixation in 3:1 acetic acid-alcohol. Specimens from all available collections of taxa

which provided material for counts have been deposited in the herbarium of Indiana University.

Hybridization Experiments

This taxonomic study was conducted using the *H. helianthoides* complex, *H. parvifolia*, *H. rubra*, and *H. annua*. The parental plants for these experiments were obtained from seed or by clone transplant. In the case of *H. annua* and *H. rubra*, the fruits were obtained from herbarium material of recent collections.

All taxa used in this study are self-incompatible for all practical purposes since only rarely did any seed set occur in self-compatibility tests. Thus, crossing races of plants was comparatively easy since emasculation was unnecessary. The immature heads were bagged before the ray flowers appeared. Pollen was transferred until all stigmas of the plant which was being used as the egg plant had withered. In this manner, seed-set percentages could be determined.

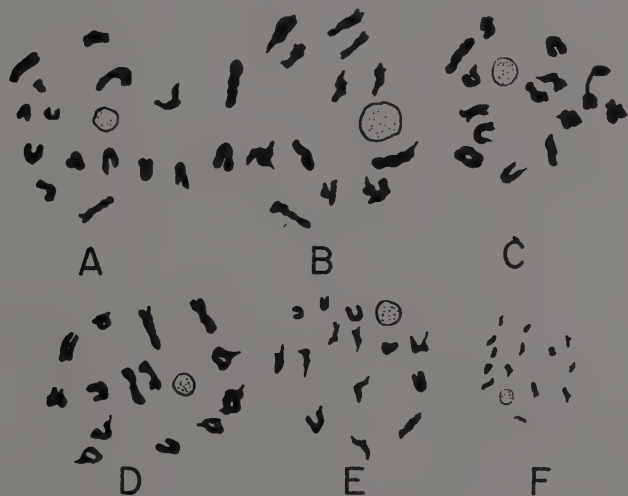


FIGURE 2. Camera lucida drawings of representative meiotic chromosome complements from pollen mother cells. (X, 1300)

- A. *H. helianthoides* (L.) Sweet ssp. *helianthoides*, Monroe Co., Indiana, Fisher 533.
- B. *H. helianthoides* (L.) Sweet ssp. *occidentalis*, St. Louis Co., Minnesota, O. Lakela s.n.
- C. *H. helianthoides* (L.) Sweet ssp. *scabra*, Franklin Co., Missouri, Fisher 410.
- D. *H. parvifolia* Gray, U. S. D. A., source unknown.
- E. *H. rubra* Fisher, Baja California, Mexico, Carter 2866.
- F. *H. annua* Hemsl., Guanajuata, Mexico, L. A. Kenoyer 2412.

As soon as the stigmas of all the disk flowers had withered, the heads were covered with cheese-cloth and tied securely an inch below the involucre bracts. These plants were left in the field until after the first frost, after which they were collected and stored in a cool, dry room.

Hybridization within the *H. helianthoides* complex was easily accomplished while interspecific crosses were made with greater difficulty (fig. 3). In the latter, the stigmas would persist, apparently indicating that the previously applied pollen did not effect fertilization. Therefore, interspecific crosses required repeated

pollinations over a longer period of time than intraspecific crosses, to insure any seed set.

Pollen viability was determined by using cotton blue in lactophenol. Those pollen grains which took a deep blue stain were counted as "good" or viable.

Interspecific Crosses

H. helianthoides ssp. *occidentalis* X *H. parvifolia*.—Only with difficulty was this cross possible and then only by repeated pollinations over a period of 10 to 14 days. Nine separate crosses, including reciprocals, were attempted during the growing season. Fertilization was effected only when *H. parvifolia* was used as the egg parent and then only 3 to 5 percent seed set was obtained. Five hybrid seedlings grew to maturity, two of which were dwarfed plants and attained a height of only 18 inches. The other plants were intermediate between the parents in most characters (table 2). The leaf base angle³ remained the same as in *H. parvifolia*. Pollen stainability was reduced from 96 percent in either parent to 34 percent in the hybrid. Fourteen bivalents were regularly present at metaphase I.

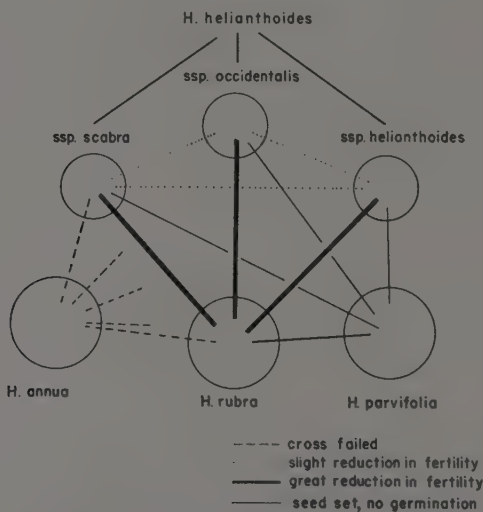


FIGURE 3. Crossing polygon showing the interfertility relationships among those *Helianthus* species used in the artificial crosses.

The dwarfed plants produced many lateral branches just above the ground level, exhibiting a growth form resembling a ball or globe. Each of the lateral branches produced many heads, which suggested the use of the plant as a possible garden ornamental. Pollen stainability was essentially the same as in the other hybrids.

These dwarfed plants were left in the field during the following winter and, like one of the parents, *H. parvifolia*, failed to survive. An attempt was made to backcross the dwarfed hybrid with the parents. The only successful cross was

³The leaf base angle was computed with a protractor by measuring the angle formed by the base of the blade and the petiole.

with *H. helianthoides* ssp. *occidentalis* as the egg parent. This yielded only two plants which morphologically resembled the egg parent more closely than the pollen parent. Pollen stainability was approximately 35 percent, no appreciable increase in viability.

In the above crosses of *H. parvifolia* with *H. helianthoides* ssp. *occidentalis*, which involved great differences in leaf shape, the deltoid-lanceolate leaf found in *H. parvifolia* appears dominant. Long peduncle also appears dominant over short peduncle, and narrow leaf over broad leaf. Other characters are intermediate between the two parents suggesting that they are the result of multiple factors

TABLE 2

Comparison of 9 characters in the parents and F_1 hybrids from inter- and intraspecific crosses in the research garden (Leaf base, angle in degrees, pubescence scored 0-glabrous to 4-dense scabrous, all other measurements in centimeters).*

Cross	Leaf base angle	Petiole length	Pubescence	Peduncle length	Leaf length	Leaf width	Ray length	Ray width	Head width	Pollen stainability
<i>H. hel. ssp. occidentalis</i> (H-3)	102	1.2	4	32.4	12.5	6.8	3.6	1.0	2.8	96%
<i>H. parvifolia</i> (H-4)	135	3.0	2	29.5	8.8	2.5	2.4	1.1	1.3	96%
Hybrid (3x4)	135	2.5	2	29.3	9.0	3.9	2.5	1.0	1.5	34%
<i>H. hel. ssp. scabra</i> (H-8)	125	1.3	4	14.0	12.0	4.0	2.3	0.9	1.5	98%
<i>H. parvifolia</i> (H-4)	135	3.0	2	29.5	8.8	2.5	2.4	1.1	1.3	96%
Hybrid (8x4)	132	2.5	2	33.0	11.0	4.7	2.3	1.1	2.1	23%
<i>H. hel. ssp. occidentalis</i> (H-3)	102	1.2	4	32.4	12.5	6.8	3.6	1.0	2.8	96%
<i>H. hel. ssp. helianthoides</i> (H-5)	135	2.5	0	6.5	11.5	5.6	2.8	0.9	1.5	99%
Hybrid (3x5)	108	1.7	3	26.2	13.4	6.3	3.2	1.0	2.2	96%
<i>H. hel. ssp. helianthoides</i> (H-5)	135	2.5	0	6.5	11.5	5.6	2.8	0.9	1.5	99%
<i>H. hel. ssp. scabra</i> (H-8)	125	1.3	4	14.0	12.0	4.0	2.3	0.9	1.5	98%
Hybrid (5x8)	125	1.3	3	12.2	11.5	5.1	3.2	0.9	1.8	93%
<i>H. hel. ssp. helianthoides</i> (H-5)	135	2.5	0	6.5	11.5	5.6	2.8	0.9	1.5	99%
<i>H. parvifolia</i> (H-4)	135	3.0	2	29.5	8.8	2.5	2.4	1.1	1.3	96%
Hybrid (5x4)	133	3.1	2	19.0	11.0	4.3	2.5	1.0	1.8	30%
<i>H. parvifolia</i> (H-4)	135	3.0	2	29.5	8.8	2.5	2.4	1.1	1.3	96%
<i>H. rubra</i> (H-16)	98	3.4	3	48.6	9.2	4.2	1.8	1.0	1.6	98%
Hybrid (4x16)	120	2.8	2	43.2	12.5	6.8	3.6	1.0	2.8	96%
<i>H. hel. ssp. occidentalis</i> (H-3)	102	1.2	4	32.4	12.5	6.8	3.6	1.0	2.8	96%
<i>H. hel. ssp. scabra</i> (H-8)	125	1.3	4	14.0	12.0	4.0	2.3	0.9	1.5	98%
Hybrid (3x8)	122	1.7	4	19.5	12.3	4.7	2.8	0.9	2.0	88%

*All characters expressed as mean values from five plants.

rather than of a single dominant one. In crosses involving other taxa, these same characters which appear dominant in the above cross are intermediate. *H. helianthoides* ssp. *occidentalis* \times *H. rubra* and the cross, *H. helianthoides* ssp. *occidentalis* \times *H. annua*, produced a few seeds by repeated crossings but germination failed.

H. helianthoides ssp. *scabra* \times *H. parvifolia*.—This hybrid exhibited lower pollen viability than the hybrid between *H. helianthoides* ssp. *occidentalis* \times *H. parvifolia*, averaging about 20 to 25 percent. When *H. parvifolia* was used as the egg parent, pollen viability averaged 25 percent, slightly higher than the reciprocal cross, which was 20 percent. This difference appears insignificant but was repeatedly observed. More striking reciprocal differences in sterility of hybrid pollen have been reported by Grant (1950) in *Gilia*.

Meiosis was observed in approximately 50 pollen mother cells and was found to be regular.

H. helianthoides ssp. *helianthoides* X *H. parvifolia*.—The five hybrids grown from this cross exhibited 30 percent pollen viability, slightly higher than ssp. *scabra* X *H. parvifolia*. No irregularities were observed in any stage of meiosis. In practically all characters this hybrid is intermediate between the two parents (table 2). This hybrid morphologically resembles ssp. *scabra* very closely.

H. parvifolia X *H. rubra*.—Seven crosses, including reciprocals, were made between these taxa. Seed set was obtained only when *H. parvifolia* was used as the egg parent, and then only 10 fruits were obtained. The following spring four seedlings grew to maturity. Meiosis in the pollen mother cells of the F₁ hybrids was highly irregular, yielding bridges, fragments, and univalents. Quite frequently three bridges and four univalents were observed at the first meiotic anaphase. Pollen stainability was found to vary from 2 to 5 percent, and seed set was less than 1 percent. None of the seeds germinated the following season.

Leaf size and head width were greater in the hybrid than in either parent (table 2). This might be attributed to hybrid vigor. *H. rubra* has red pales while in *H. parvifolia* they are yellowish-brown. In all four hybrids the pales were yellowish-brown, suggesting that the red pale color in *H. rubra* is due to a recessive gene or genes. The hybrids resemble the egg parent, *H. parvifolia*, more closely than *H. rubra*.

All attempts to cross *H. annua* with other taxa under cultivation in the research garden failed.

Intraspecific Crosses in H. helianthoides

H. helianthoides ssp. *occidentalis* X ssp. *scabra*.—In this F₁ hybrid the leaf base-petiole angle and petiole length are greater than in either parent, while other characters are intermediate (table 2). Pollen viability was decreased to 88 percent, only a slight decrease from 96 percent in ssp. *occidentalis* and 98 percent in ssp. *scabra* (fig. 3). The cross was easily made, that is, the stigmas withered soon after pollen was applied and seed set was as high as in either parent. The chromosomes exhibited good pairing at meiosis. This hybrid resembles many specimens of northwest Missouri, southwest Iowa and northeast Kansas, a region in which the two subspecies overlap in their natural distributions. For this reason many herbarium specimens have been annotated as putative hybrids.

The two remaining crosses, ssp. *occidentalis* X ssp. *helianthoides* and ssp. *helianthoides* X ssp. *scabra*, were easily made in the research garden with a slight decrease in pollen viability of the hybrids. Most characters measured were intermediate between those of the two parents (table 2).

Discussion of Crosses

Although *H. parvifolia* and *H. rubra* exhibit several morphological similarities, they are geographically and reproductively isolated. Their artificial hybrids yield only 3 to 5 percent viable pollen which would be expected since meiosis is highly irregular. *H. parvifolia* appears more closely related to *H. helianthoides* since their artificial hybrids yield higher average pollen fertility (23 to 34 percent). *H. rubra* fails to cross with any subspecies of *H. helianthoides*, suggesting a closer relationship to *H. parvifolia* than to any other species used in this study.

There are apparently no reproductive barriers to crossing within the *H. helianthoides* complex. Hybrids have been easily made between the subspecies, and pollen fertility is almost as high as in the parental types.

H. helianthoides ssp. *scabra* resembles the hybrid between *H. helianthoides* ssp. *helianthoides* and *H. parvifolia* very closely, suggesting that ssp. *scabra* may owe its origin to hybridization of these taxa at some time in their evolutionary history.

H. annua repeatedly failed to cross with any other species grown in the research garden, indicating complete reproductive isolation.

Ornamental and Economic Importance

There are several named varieties of *Heliopsis* which are grown as ornamentals. The varieties available for this study were *Heliopsis Gold Everhart*, *Heliopsis Pitcheriana*, *Heliopsis scabra* var. *incomparabilis*, and *Heliopsis helianthoides* var. *zinnaeflorae*. All of these horticultural varieties, with the exception of *Heliopsis helianthoides* var. *zinnaeflorae*, were grown and observed in the research garden. Meiosis in pollen mother cells was examined and found to be regular.

The above named varieties are not included in the taxonomic treatment of the genus because their affinities could not easily be established. *Heliopsis Gold Everhart* is very similar to *H. helianthoides* ssp. *occidentalis*, differing only in having about twice as many ray flowers. *Heliopsis Pitcheriana* is very similar to *H. helianthoides* ssp. *helianthoides*, differing in being slightly larger. *Heliopsis scabra* var. *incomparabilis* is obviously closely related to *H. helianthoides* ssp. *occidentalis*. From herbarium specimens of *H. helianthoides* var. *zinnaeflorae* it is apparent that it is also very close to *H. helianthoides* var. *occidentalis*.

The most striking differences between the horticultural varieties and the wild taxa are the larger size, greater number of ray flowers, and longer peduncles. These characters are those most likely to be selected by the horticulturist.

In 1943 and 1944, the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture isolated an insecticidal amide from the roots of a Mexican plant referred to as *Erigeron affinis* DC. In 1946, E. L. Little, Jr., of the Foreign Economic Administration, called attention to the confusion in the botanical classification of the Mexican "peritre del pais" ("native pyrethrum") and pointed out that the plant was actually *Heliopsis longipes* (Gray) Blake, common name "chilcaugue" or "chilcuan" (Martin, Acree and Haller, 1947).

Since 1944, a larger supply of roots has been obtained from Mexico which provided an abundance of the insecticidal amide (N-isobutyl-2, 6, 8-decatrienamide). An investigation was undertaken by the United States Department of Agriculture to determine the insecticidal activity of *Heliopsis* native to the United States, and it was found that all of these taxa, namely, *H. helianthoides* ssp. *scabra*, *H. gracilis* and *H. helianthoides* ssp. *helianthoides*, particularly the roots, were toxic to house flies. The roots of *H. helianthoides* ssp. *scabra* were especially toxic to these insects (Gersdorff, 1950). The pungent isobutylamide, for which the Department of Agriculture has proposed the name "scabrin," is appreciably more toxic than pyrethrins to most insects.

Generic Relationships

The genus *Heliopsis* has been associated with *Zinnia*, *Philactis*, *Eclipta*, and *Sanvitalia* by virtue of their opposite leaves, pistillate, fertile, and persistent ray flowers, and hermaphroditic, fertile disk flowers. The major differences separating these species from *Heliopsis*, however, are striking; narrow and usually entire leaves, phyllaries in 3-5 series, 3-angled ray achenes, flattened disk achenes, and a pappus, if present, of 1-several teeth.

*Taxonomy*⁴

⁴The herbaria from which material has been available for study are indicated by the following abbreviations: PH—Academy of Natural Sciences of Philadelphia Herbarium; F—Chicago Natural History Museum (Field Museum); GH—Gray Herbarium, Harvard University; IND—Indiana University Herbarium including the C. C. Deam Herbarium; MO—Missouri Botanical Garden Herbarium; NY—New York Botanical Garden Herbarium; SMU—Southern Methodist University Herbarium; US—United States National Herbarium, Smithsonian Institution, Washington, D. C.; UC—University of California Herbarium, Berkeley; MICH—University of Michigan, Ann Arbor; MIN—University of Minnesota, Minneapolis; TEX—University of Texas Herbarium, Austin. The writer wishes to express appreciation to the curators of the above listed herbaria.

Heliopsis Persoon*Heliopsis* Pers., Syn. 2: 473. 1807.*Callais* Cass., Dict. Sc. Nat. 24: 327. 1822.*Helepta* Rafin., Neogynt. 3: 1825.*Andrieuxia* DC., Prodr. 5: 559. 1836.*Helenomoium* Willd., ex DC. Prodr. 5: 551. 1836.

Roots perennial or annual, somewhat fleshy, fusiform; aerial stems erect and ascending, or prostrate, leafy, branched, glabrous or variously pubescent. *Leaves* opposite or rarely alternate, filiform, lanceolate, orbicular, ovate, ovate-lanceolate, deltoid or deltoid-ovate, glabrous or variously pubescent, margin irregularly dentate to nearly entire, nearly sessile or with petioles up to 3.5 cm. long. *Heads* usually rather large, 0.6–3.5 cm. wide, terminal and from axils of upper leaves, radiate and discoid. *Phyllaries* 2–3 seriate, herbaceous or coriaceous, ovate-lanceolate to ovate, subequal, outer series often foliaceous and longer than disk. *Receptacle* rather broadly convex, often hollow; pales firm, conduplicate, persisting, light brownish-yellow, red or purple. *Disk-flowers* perfect, yellowish, brownish-yellow or purple; ray-flowers pistillate and fertile, yellow, orange-yellow, or purple, ovate-lanceolate to oblong-lanceolate, notched at the apex, persistent. *Achenes* of the disk-flowers fertile, quadrangular at apex, conical at base, glabrous or minutely pubescent, those of the ray-flowers triangular, outer surface convex, otherwise as the disk achenes. *Pappus* lacking or represented by 2–3 membranaceous teeth or merely a crenulate ridge.

Type Species: *Bupthalamum helianthoides* L. Sp. Pl. 2: 904. 1753.

Artificial Key to the Species

- A. Pales of the disk red or purplish-black
 - B. Rays yellow
 - C. Peduncles 30–40 cm. long, heads 1.0–1.5 cm. wide, pales red, axils of lateral branches and leaves densely tomentose; Baja California, Mexico.1. *H. rubra*
 - C. Peduncles 5–10 cm. long, heads 0.6–0.8 cm. wide, pales purple, axils of lateral branches and leaves sparingly pubescent; Michoacan, Mexico.2. *H. brachactis*
 - B. Rays purple, peduncles 2.5–5.5 cm. long, pales purplish-black, heads 0.3–0.5 cm. wide; Guerrero, Mexico.3. *H. parviceps*
- A. Pales of the disk yellow or yellowish-brown
 - B. Plants prostrate or semi-prostrate
 - C. Leaves ovate-oblong to generally orbicular, peduncles 12.0–15.0 cm. long, phyllaries 1.1–1.3 cm. long; southern Mexico.4. *H. procumbens*
 - C. Leaves lanceolate, peduncles 4.0–7.0 cm. long, phyllaries 0.7–0.8 cm. long; Peru.5. *H. decumbens*
 - B. Plants erect
 - D. Rays 6–8
 - E. Leaves glabrous, sessile or petiolate
 - F. Leaves sessile, filiform. Coahuila, Mexico.6. *H. filifolia*
 - F. Leaves petioled, ovate to ovate-lanceolate
 - G. Plants 50–75 cm. tall, branched, petioles 2.5–3.5 cm. long; Mexico, Central and South America.7. *H. bupthalamoides*
 - G. Plants 30–40 cm. tall, usually monocephalous, petioles 0.8–1.0 cm. long; southeastern United States.8. *H. gracilis*
 - E. Leaves pubescent, petiolate
 - H. Leaves orbicular or ovate-lanceolate, peduncles 9–20 cm. long
 - I. Leaves 1.0–2.3 cm. wide, 2.0–3.0 cm. long, heads less than 1.0 cm. wide, plants 30.0–35.0 cm. tall; San Luis Potosi, Mexico.9. *H. longipes*
 - I. Leaves 2.5–4.5 cm. wide, 4.5–9.5 cm. long, heads 0.8–1.2 cm. wide, plants 50.0–75.0 cm. tall; Mexico, Central and South America.7. *H. bupthalamoides*
 - H. Leaves deltoid to deltoid-ovate, peduncles 5.5–7.5 cm. long; Central Mexico.10. *H. annua*
 - D. Rays 10–18
 - J. Achenes rugose to subtuberculate, tan or black
 - K. Leaves deltoid-lanceolate, petioles 0.8–2.5 cm. long, achenes black, plants 30–40 cm. tall; southwest United States and northern Mexico.11. *H. parvifolia*
 - K. Leaves ovate to ovate-lanceolate, petioles 2.5–3.5 cm. long, achenes light tan, plants 50–70 cm. tall; north central Mexico to Bolivia.7. *H. bupthalamoides*

- J. Achenes smooth, brown to dark brown
 L. Leaves lanceolate, 5.8–8.5 cm. long, 1.0–1.8 cm. wide, leaves and peduncles densely pilose; Colombia.....12. *H. lanceolata*
 L. Leaves ovate-lanceolate to deltoid 8.0–12.0 cm. long, 3.0–6.0 cm. wide, leaves and peduncles glabrous to rough scabrous. Central and eastern United States.....13. *H. helianthoides*

1. *Heliopsis rubra* Fisher, Madrono 12: 152–155, 1954. (T.: Carter & Kellogg 3158 UC! Isotype IU!)

Errect or ascending annual, biennial or perennial herb in mountainous regions, annual in plains region, 50–75 cm. tall, branching nearly to woody base; stems 0.5–3.5 mm. thick, glabrous below, sparingly pubescent above, previous year's stems glaucous, periderm flaking with age; axils of lateral branches and leaves densely tomentose; internodes 3.5–6.5 cm. long; leaves 6.5–

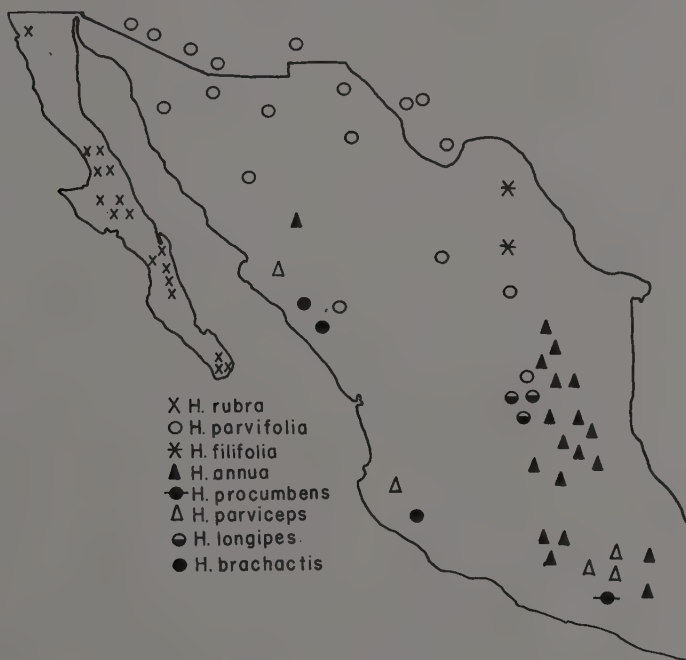


FIGURE 4. Distribution of Mexican species of *Heliopsis*.

12.0 cm. long, 3.5–5.0 cm. wide, firm, light green below, darker green above, petioles slender, 3.5–5.5 cm. long, tomentose, lower surfaces of blades glandular hirsute, densely strigose on the veins, upper surface glandular hirsute, rather scabrous, blades deltoid-rhomboid, apex acuminate, base attenuate to obtuse, margin nearly entire or sparingly dentate, teeth acute and mucronate; peduncles 30.0–40.0 cm. long; heads (excluding rays) 1.0–1.5 cm. wide (in fruit); involucre 2-seriate, phyllaries appressed, the outer unequal, oblong to oblong-lanceolate, apex acuminate to acute, densely velutinous to sericeous on the outer surface extending downward onto the upper limit of the peduncle; the inner phyllaries shorter and more acuminate; rays 8–10, 14–21 cm. long, 6–8 mm. wide, 13–15 nerved, yellow below at anthesis, reddish-orange above, becoming dull yellow with conspicuous greenish, sparingly pubescent nerves below and golden yellow above at maturity; disk corollas yellowish, lobes sparingly pubescent at the apex, tube 4.0–4.5

mm. long (at anthesis), obtuse; *pales* lanceolate-oblong to spatulate, glabrous, red at apex when young, becoming brownish-orange with age, membranaceous along the margins, 7.0–7.5 mm. long, 1.5–2.0 mm. wide; *ray achenes* triangular, outer surface curved, slightly puberulous when young, 4.0–4.5 mm. long, 2–3 nerved, surface irregularly tuberculate; *disk achenes* quadrangular, sharply so at the apex, rounded at the base, epappose or slightly ridged, faintly nerved on the angles.

Type locality.—Mexico: Baja California: Distrito del Sur, El Pulpito del Arroyo de las Parras, Sierra de la Giganta, lat. 25°58' N., long. 111°29' W., north-facing slopes, altitude 250 m.

Distribution.—Costal plains and mountainous regions of Baja California, Mexico (fig. 4). October to April.

In the past, herbarium material of *H. rubra* has been annotated as *H. parvifolia* which it resembles very closely and undoubtedly is its nearest relative. The chief separating characters are found in the leaf size, the shape to a lesser extent, and the color of the chaff.

According to Annetta Carter (correspondence), who has collected in the vicinity of the type locality on several occasions, *H. rubra* is a biennial or perennial herb in mountainous regions but grows as an annual in plains regions. In the mountains it usually occurs on north-facing slopes or breaks in vertical canyon walls. In years of good late summer rains it may be abundant in full sun on open plains, while in poor years these areas support little or no annual vegetation and may be covered with drifting sand.

2. *Heliopsis brachactis* Standl. ex Fisher sp. nov. (T.: Leavenworth & Hoogstraal 1370 MO!)

Herba annua, erecta; folia ovato-deltoida, sparse pubescentia, 7.5–10.0 cm. longa, 3.0–4.5 cm. lata; petiolis 2.5–4.0 cm. longis, glabris; capitula 6.0–8.0 mm. lata, radii 4–5, aurei; corollae disci 2.0–3.0 mm. longae, purpureae, paleae 3.0–3.5 mm. longae, purpureae; achenia radii triangularia, 3.0–3.5 mm. longa, tuberculata; achenia disci quadrangularia 2.5–3.0 mm. longa.

Slender annual, 40–50 cm. tall; *stems* glabrous except in axils of upper leaves, 2.0–2.5 mm. thick, internodes 8.0–10.0 cm. long below, 3.0–5.5 cm. long above; *leaves* ovate to deltoid, firm, 7.5–10.0 cm. long, 3.0–4.5 cm. wide, crenate to subdentate, upper and lower surface slightly scabrous; *petioles* 2.5–4.0 cm. long, glabrous; *peduncles* of mature heads 5.0–10.0 cm. long, glabrous to minutely pubescent; *heads* small 6.0–8.0 mm. wide; *involucre* biseriate, outer phyllaries greenish, somewhat foliaceous, linear-oblong, inner oblong to obovate; *rays* 4–5, yellow, 5.0–6.0 mm. long, 2.0–3.0 mm. wide, commonly 2-cleft; *disk corollas* 2.0–3.0 mm. long, lobes purplish-black, *pales* 3.0–3.5 mm. long, suffused with purple at apex; *disk achenes* quadrangular 2.5–3.0 mm. long, dark brown, tuberculate, sharply angled, epappose; *ray achenes* obovoid, 3.0–3.5 mm. long.

Type locality.—Mexico: Michoacán: region of Tancitaro, 4 miles west of Apatzingan in semi-desert area, elevation 1200 feet. This species is known only from type locality.

Although *H. brachactis* differs strikingly from all other species in the genus, *H. parviceps* or *H. annua* seem to be the closest relative.

3. *Heliopsis parviceps* Blake, Proc. Biol. Soc. Wash. 33: 268, 1943. (T.: L. H. MacDaniels 128 F!)

Slender herbaceous annual, 45–60 cm. tall, with elongate branches above; *stem* light green, 1.5–1.8 mm. thick, striate; *leaves* small, ovate, 3.0–4.0 cm. long, 1.2–1.7 cm. wide, evenly hirsute on both surfaces, irregularly dentate to entire; *petioles* slender, 0.8–1.5 cm. long, pilose on the margins; mature branches with internodes up to 18 cm. long; *peduncles* 2.5–5.5 cm. long, glabrous to minute pubescent above; *heads* 0.3–0.5 cm. wide; *involucre* 2-seriate, phyllaries, 10–12, subequal 6.0–8.0 mm. long, the outer oblong, obtuse, 1.5–1.8 mm. wide, the inner broadly ovate, obtuse, all sparingly puberulous, strongly suffused with purple at maturity; *rays* 4–5, spreading, deep purple on both sides, finely papillate on both surfaces, margins inflexed forming a short tube or ring 3.0 mm. long above the achene, bluntly 3-cleft, 10–12 nerved, hispidulous on the nerves and the ring-like base; *disk corollas* deep purple, glabrous, about 3.0 mm. long, lobes ovate, acute, 0.6 mm. long; *pales* membranaceous, 3.5–4.5 mm. long, purple above, glabrous, keeled for $\frac{2}{3}$ of the length from the base then broadly rounded and bluntly mucronate; *ray achenes* broadly obovoid, epappose, papillate and somewhat tuberculate, 3.0–3.5 mm. long, 2.3–2.5 mm.

wide, rounded on the outer face; *disk achenes* oblong, epappose, papillate to tuberculate, truncate at apex.

Type locality.—Mexico: Guerrero: along Cuernavaca-Taxco Road, 10 miles from Taxco, 5500 feet elevation.

Distribution.—Known only from the type locality (fig. 4).

This species is easily distinguished by its slender habit, small leaves, and purple disk and ray flowers. Although there are many differences, *H. brachactis* seems to be the nearest relative of this species.

4. *Heliopsis procumbens* Hemsl., Biol. Centr-amer. 2: 156, 1882. (T.: *M. Borgeau* 837 Kew, isotype GHI)

Prostrate creeping perennial herb, much branched, 20–25 cm. tall, leafy to base; *roots* thick, coarse, fibrous; *stems* 1.0–1.5 mm. thick, villous, internodes 2.0–2.5 cm. long; *leaves* orbicular or rarely ovate-oblong, 1.2–2.3 cm. wide, 2.0–3.0 cm. long, acute to obtuse at apex, lower and upper surfaces equally sericeous pubescent, sessile or with petioles to 5 mm. long, subterete; *peduncles* 12.0–15.0 cm. long, evenly sericeous pubescent; *heads* 0.9–1.2 cm. wide, 1.1–1.2 cm. high (as pressed); *involucre* 2-seriate, the outer phyllaries exceeding the inner, herbaceous, oblong, obtuse, glabrous, the inner more linear, acute tipped, glabrous; *rays* 8–10, 4.0–4.2 mm. wide, 0.8–1.1 cm. long, glabrous, golden yellow, irregularly 2–3 cleft; *disk corollas* 2.0–3.0 mm. long, glabrous, lobes golden yellow, obtuse; *pales* linear, 1.5–2.0 mm. wide, 3.5–4.0 mm. long, membranaceous along margins, keeled, acuminate; *achenes* epappose; *ray achenes* triangular, glabrous, smooth; *disk achenes* quadrangular, slightly tuberculate, tannish-brown when mature.

Type locality.—The handwriting on the label of the isotype is almost illegible, but appears to read "elevated pasture in forests, Desierta Vija." It is difficult to tell whether Disierta Vija is meant to indicate a city or a general locality. At any rate, the type locality was not located. Hemsley, in describing the species, presumably from the holotype, refers to Disierto Viejo of South Mexico. The holotype was not available for study by the writer, but Dr. H. J. Brodie, Botany Department, Indiana University, examined the type specimen and verified the description.

Distribution.—From north central Sinaloa south to Jalisco, southeast to the state of Mexico, at elevations up to 10,000 feet (fig. 4). June through September.

5. *Heliopsis decumbens* Blake, Proc. Biol. Soc. Wash. 53: 72, 1940. (T.: *W. H. Osgood* and *M. P. Anderson* 35 F!)

Low perennial herb with prostrate branching rhizome, short decumbent stems and long ascending or erect terminal peduncles; *stems* subterete, striate, pilose; internodes 5.0–10.0 mm. long; *leaves* ovate-lanceolate, 2.5–3.5 cm. long, 1.0–1.5 cm. wide, obtuse, cuneate, margin crenate-serrate, lower surface hirsute on main veins, sparingly so on smaller veins and other surfaces, densely hirsute on margins, upper surface glabrous or sparingly hirsute, *petioles* broad, 5.0–7.0 mm. long, pilose, obscurely margined to base; *peduncles* 4.0–7.0 cm. long, slender, pilose, with spreading or upcurved hairs, densely so beneath the head; *heads* 3.0–3.5 cm. wide, 1.5–2.0 cm. high (as pressed); *involucre* 2-seriate, outer phyllaries, 7.0–10.0 mm. long, oblong to oblong-ovate, obtuse, callose tipped, spreading to rather densely pilose with spreading or erect hairs, subindurate toward base, *inner phyllaries* 6.0–8.0 mm. long, obtuse or short acute, sparingly pubescent to nearly glabrous; *receptacle* (in flower) short, conical; *rays* 13–15, 1.0–1.3 cm. long, 0.3 cm. wide, golden yellow, oblong, 3-cleft, 11–14 nerved, hispidulous at the base; *disk corollas* yellow, glabrous, 4.0–6.0 mm. long; *pales* scarious, obtuse or acute, narrowly keeled, 3 nerved, about 6.0 mm. long; *ray achenes* obovoid-triangular, glabrous, epappose, 3 mm. long, 1.5 mm. wide, 1–3 nerved on each face, with narrow whitish irregular undulate margins; *disk achenes* obovoid, compressed, thickened, faintly three-nerved on each side, brownish to blackish, glabrous, epappose, quadrangular at the apex, 2.7 mm. long, 1.0–1.3 mm. wide.

Type locality.—Peru: Cajamaraca.

Distribution.—This species is known only from type locality. Although only a few specimens were available for examination, they are sufficiently distinct on the basis of its prostrate

habit, short peduncles and pubescence to warrant recognition as a species. It is impossible to ascertain its nearest relative from the few specimens available.

6. *Heliopsis filifolia* S. Wats., Proc. Amer. Acad. Sci. 25: 153, 1890. (T.: C. G. Pringle 2396 US!)

Erect perennial herb, 15.0–25.0 cm. tall, leafy branched to base; *stems* 1.5–2.5 cm. thick, glabrous, terete, smooth; internodes 1.5–3.0 cm. long; *leaves* filiform, sessile, fascicled, opposite below, often alternate above, blade 2.0–2.5 cm. long, 1.0–1.5 mm. wide, pale green to straw-colored when dry, minutely strigose below, margin entire, apex obtuse; *peduncles* 13.0–30.0 cm. long, glabrous, terete; *heads* 1.5–2.0 cm. wide, 1.0–1.5 cm. high (as pressed); *involucre* 2-seriate, the inner phyllaries slightly exceeding the outer, tomentose along margins, 4–6 nerved, acute; *rays* elliptical, 1.5–1.8 cm. long, 1.0–1.5 cm. wide, 8–10 nerved, 1–3 cleft at apex, golden yellow, glabrous; *disk corollas* 6.0–6.5 mm. long, greenish-yellow below, bright yellow above, glabrous, lobes acute; *pales* 1.0–1.2 mm. wide, 1.0–1.2 cm. long, linear, 1–4 nerved, membranaceous along margins, brownish yellow above, apex broadly acute; *ray achenes* triangular, outer face curved, sparingly strigose, slightly rugulose, epappose; *disk achenes* quadrangular, truncate, rounded below, rugulose, strigose pubescent, epappose.

Type locality.—Mexico: Coahuila: Carneros Pass on limestone hills and ridges (fig. 4).

This relatively homogeneous species is very distinct by virtue of its filiform, sessile leaves, and glabrous peduncles. It is difficult to assign affinities to this taxon since there is only slight resemblance to any other species in the genus.

7. *Heliopsis bupthalmoides* (Jacq.) Dunal. Mem. Mus. Paris 5:56, 1819.

Anthemis bupthalmoides Jacq., Hort. Schoenb. 2: 13, 1797. (T.: British Museum.)

Heliopsis canescens Don. Bot. Reg. t. 7: 592, 1821. (T.: Humboldt & Bonpland s.n. Paris Museum.)

Andrieuxia Mexicana DC. Prodr. 5: 559, 1836. (T.: Geneva Museum, Photograph examined US!)

Perennial herb 50.0–75.0 cm. tall, much branched; *stems* terete, glabrous to pubescent above, pubescence often in two lines on opposite sides of the stem; internodes 7.5–12.5 cm. long; leaves ovate to ovate-lanceolate, cuneate to near truncate at base, 4.5–9.5 cm. long, 2.5–4.5 cm. wide, veins on lower surface sparingly to rather densely pubescent; *petioles* slender, 2.5–3.5 cm. long, sparingly to densely pubescent; peduncles 10.0–14.5 cm. long, essentially glabrous or pubescent in lines below the head; *heads* 0.8–1.2 cm. wide; involucre mostly 2-seriate, phyllaries oblong-lanceolate, acute to obtuse, essentially glabrous to villous, rarely leafy; *rays* 8–10, yellow, 2.5–3.0 cm. long, 0.5–1.0 cm. wide, linear-oblong, irregular 3-cleft; *disk corollas* yellowish-brown; *pales* linear-oblong, yellowish-brown; *achenes* tan to light brown at maturity, rugose, obovoid, epappose.

Distribution.—This species has, by far, the most widespread distribution of any in the genus, ranging from north central Mexico south through Central America into South America as far as central Bolivia (fig. 5). It has been collected at altitudes ranging from 600 to 10,000 feet.

Heliopsis bupthalmoides is a wide-ranging species and, as might be expected, there is considerable variation, particularly in leaf shape and amount of pubescence. Until more material from South America is available, it seems advisable to place *H. canescens* in synonymy with *H. bupthalmoides* since the diagnostic characters utilized in the original description fail to separate the two taxa clearly.

Heliopsis canescens was described from material collected and observed by Humboldt and Bonpland in the vicinity of Loxa, near Quito, Ecuador. Their reason for giving the taxon specific status was based on the nature of the pubescence of the leaves, upper stems and involucre. These characters are not consistent throughout the range of the species. Generally the pubescence of this taxon is most dense in the southernmost portion of the range and becomes less dense in the tropical portions of South America and Central America. Finally, in the northernmost portions of the range in Mexico, the taxon is nearly glabrous. It has also been observed that the truncate leaf shape is more generally found in specimens with the greatest amount of pubescence.

H. buphthalmoides resembles no other species in Mexico, Central or South America. It is morphologically more closely related to *H. helianthoides* of the United States in general habit, leaf shape, and size.

8. *Heliopsis gracilis* Nutt. Trans. Amer. Phil. Soc. N. S. 7: 353, 1841.

Heliopsis laevis var. *gracilis*. Torrey and Gray, Fl. No. Amer. 2: 303, 1842.

Erect perennial herb, 30–40 cm. tall, slender, unbranched to sparingly branched; *stems* 1.0–1.5 mm. thick, glabrous, smooth; *leaves* ovate-lanceolate to lanceolate, 4.5–5.5 cm. long, blade 1.8–2.0 cm. wide, light green below, deep green above, lower surface glabrous, upper surface sparingly strigose, more dense along margins, blade somewhat cuneate at base, acuminate at the



FIGURE 5. Distribution of *H. buphthalmoides*.

apex, nearly regular dentate, teeth averaging 1.0 mm. long, *petioles* 0.8–1.0 cm. long, glabrous to sparingly pubescent, somewhat subterete; *peduncles* 15.0–22.0 cm. long, glabrous below, minutely pubescent above; *heads* small, 1.0–1.2 cm. wide, 0.7–1.0 cm. high (as pressed); *involucre* 2-seriate, minutely pubescent on back, becoming more dense along margins, the outer phyllaries slightly foliaceous, spreading, linear-oblong, obtuse at apex, the inner phyllaries shorter, linear, obtuse; *rays* 6–8, linear, glabrous, 5.0–8.0 mm. wide, 1.8–2.2 cm. long, 1–3 cleft at apex, golden yellow; *disk corollas* 3.5–4.0 mm. long, throat pale brownish-yellow, glabrous, lobes dull yellow; *pales* lanceolate, keeled, 0.8–1.0 cm. long, obtuse; *achenes* glabrous to minutely pubescent on margins, dull brown, pappus a laciniate crown or 1–3 pointed teeth, ray achenes triangular; *disk achenes* quadrangular.

Type locality.—The type specimen is thought to be deposited in the British Museum and was not available for study. From a note penned on a herbarium sheet by Asa Gray, and by information obtained from the original description, the type locality must be in the southeast United States, probably Florida, Georgia, or Alabama.

Distribution.—From southwest Georgia west through north central Florida to southern Alabama (fig. 6).

The original description adequately agrees with the specimens examined except for a ref-

erence made concerning the indument of the leaves and peduncles which is described as being scabrous or smooth. The description may have been compiled from a single plant specimen. All the herbarium specimens examined are glabrous, or essentially so, certainly not scabrous. The most logical explanation of this discrepancy lies in the fact that the range of the species, as cited in the original description, is Georgia to Louisiana to Arkansas. This range would overlap that of the newly described taxon *H. helianthoides* ssp. *scabra*, which does have scabrous leaves. All specimens from Louisiana to Arkansas have been determined *H. helianthoides* ssp. *scabra*, not *H. gracilis*. Therefore the original description by Nuttall may have been broadened to include those plants which are now determined *H. helianthoides* ssp. *scabra*.

Heliopsis gracilis was not grown or observed in the living condition during this investigation. Morphologically, *H. gracilis* resembles *H. helianthoides* ssp. *helianthoides* in most respects except for size, ecological preference and non-branching habit. This species has been reported most often growing in well shaded areas, namely pine barrens.

9. *Heliopsis longipes* (Gray) Blake, Contr. U. S. Nat. Herb. 22: 608, 1924.

Philactis longipes Gray, Proc. Amer. Acad. Sci. 15: 35, 1879. (T.: C. C. Perry & E. Palmer 465 F!)

Subdecumbent or erect perennial herb, sparingly branched from the base; roots thick, coarse, fibrous; *stems* 1.0–1.5 cm. thick, glabrous below, sparingly to densely scabrous above; internodes 2.0–5.5 cm. long; *leaves* 2.0–3.0 cm. long, 1.0–2.3 cm. wide, oblong-lanceolate to elliptical, *petioles* 1.0–2.5 mm. long, strigose, blades irregularly dentate to entire above, about equally acute to obtuse at apex; *peduncles* 9.0–20.0 cm. long, sparingly pubescent below to densely pubescent above; *heads* (immature) 0.6–0.9 cm. wide, 0.9–1.2 cm. high; *involucre* 2-seriate, outer phyllaries densely pubescent on back, glabrous on inner side, obtuse, the inner phyllaries shorter, glabrous, acuminate at apex; rays 6–8, linear-oblong, 2–3 cleft, about 0.3 cm. wide, 1.0–1.2 cm. long, sparingly pubescent on back, yellow; *disk corolla* about 3 mm. long, glabrous, brownish-yellow above; *pales* linear-lanceolate, yellowish-brown, about 1.0 mm. wide, 1.0 cm. long, faintly 4 nerved, acuminate, glabrous; *ray achenes* (immature) triangular, glabrous; *disk achenes* (immature) quadrangular, glabrous, epappose or pappus of 2–3 minute, membranaceous awns.

Type locality.—Mexico: San Luis Potosi: Altitude 6000–8000 feet.

Distribution.—Known only from San Luis Potosi, Mexico (fig. 4).

Only three herbarium specimens were available for study but the taxon appears distinct by its small lanceolate-oblong, strigose leaves with very short petioles. It is further characterized by having rather long peduncles with small heads.

10. *Heliopsis annua* Hemsley, Biol. Centr. Amer. Bor. 2: 56, 1881. (T.: Coulter 358 Kew)

Erect, annual herb, much branched, 25.0–40.0 cm. tall; *stems* 2.5–4.5 mm. thick, striate, sparingly pubescent in vertical lines above; internodes 5.0–12.0 cm. long; *leaves* deltoid to ovate, 4.5–7.7 cm. long, 2.2–4.0 cm. wide, pale green below, light green above, sparingly pubescent below and above, margin irregularly dentate or crenulate to entire above; *petioles* long and slender, 2.5–3.5 cm. long, *peduncles* 2.5–7.5 cm. long, striate with two vertical lines of pubescence to apex, essentially glabrous elsewhere; *heads* 1.0–1.5 cm. wide, 0.8–1.2 cm. high; *involucre* 2-seriate, the outer phyllaries somewhat spreading and foliar, linear-oblong, acute and submucronate, pubescent on outer surface and margin, inner surface glabrous, the inner phyllaries membranaceous, 2–3 nerved, pubescent on margins, obtuse; *rays* 8–10, yellow, 5.0–6.0 mm. wide, 1.0–1.5 cm. long, 7–10 nerved on back, apex irregularly 3-cleft; *pales* 2.0 mm. wide, 5.0–7.0 mm. long, glabrous, faintly keeled, membranaceous, obtuse, cream yellow at apex; *ray achenes* triangular, epappose, outer surface convex, rounded at base, truncate at apex, glabrous, subtuberculate; *disk achenes* quadrangular, epappose, abruptly truncate at apex, glabrous below, sparingly pubescent above.

Type locality.—Mexico: Zacatecas: near Zacatecas.

Distribution.—Mexico: Southeast Sonora south to Michoacan and Queretaro, north to San Luis Potosi (fig. 4). July through September.

Dr. H. J. Brodie, Botany Department, Indiana University, examined the type specimen at Kew and found it to agree with the description. The taxon is distinct and easily recognized

by its many, compact showy heads on rather short peduncles, and the soft evenly pubescent leaves. In some localities this annual species is a weed in gardens and fields, whereas in other localities it is rather rare. Some collections indicate that it grows at altitudes of 7,000 meters. In the research garden at Indiana University, it exhibited prolific growth, spreading over an area of 3 to 4 feet. The attempted production of artificial hybrids with *H. parvifolia*, *H. rubra*, and *H. helianthoides* was unsuccessful. The taxon is relatively homogeneous. Its nearest relative seems to be *H. parvifolia* although it differs strikingly.

11. *Heliopsis parvifolia* Gray, Smithson. Contr. Knowl. (Pl. Wright.) 2: 86, 1853. (T.: *C. Wright* 1218 NY!)

Erect perennial herb, 30–40 cm. tall, slender; *stems* 1.5–4.0 mm. thick, glabrous or sparingly pubescent below, striate; internodes 1.5–7.5 cm. long; *leaves* deltoid-lanceolate, approaching deltoid-ovate, blade 1.5–5.5 cm. long, 0.8–1.5 cm. wide, light green below to deep green above becoming straw colored when dry, both surfaces sparingly pubescent to nearly glabrous, margin irregularly dentate to nearly entire, the lowermost teeth usually larger and irregular, decurrent or tapering abruptly onto petiole, apex acuminate to obtuse, *petioles* 0.8–2.5 cm. long, slender, puberulous; *peduncles* 8.5–20.0 cm. long, pubescent, apex more or less enlarged and hollow; *heads* 1.2–2.0 cm. wide (as pressed), disk 0.8–1.0 cm. high; involucre 2-seriate, the outer phyllaries exceeding the inner, oblong to oblong-lanceolate, apex acuminate, 4–6 nerved, densely pubescent on margins; *rays* 9–11, 1.2–1.4 cm. wide, 2.7–2.9 cm. long, oblong-ovate, 7–9 nerved, 3-cleft, glabrous, golden yellow when young, pale yellow with age, *disk corollas* yellowish-brown, glabrous, 4.0–4.5 mm. long, lobes brighter yellow than tube, obtuse; *pales* lanceolate to oblong, glabrous, keeled, acuminate at apex, 8.5–9.0 mm. long, yellow tipped; *ray achenes* epappose, 4.5–5.0 mm. long, brownish-black, triangular, glabrous, rugulose, faintly nerved on each face; *disk achenes* epappose, quadrangular, brownish-black when mature, 4.0–4.5 mm. long.

Type locality.—Mexico: Sonora: Hillsides between Barbacomori and Santa Cruz.

Distribution.—Southwest Texas to southeastern Arizona, southward to Durango and east to Tamaulipas, Mexico (fig. 4). June through October.

The species appears to be relatively homogenous and can easily be identified by leaf characters. The lower teeth of the serrate leaf are large and long, giving the leaf a deltoid shape (fig. 1). In addition to this, the peduncles are among the longest in the genus, reaching 20 cm. and amounting to half the total height of the plant. Under cultivation in the Indiana University experimental gardens, this species shows extreme vigor, attaining approximately twice the size exhibited by herbarium material.

12. *Heliopsis lanceolata* Blake, Proc. Biol. Soc. Wash. 53: 71, 1940. (T.: *E. P. Killip* and *E. C. Smith* 17339 US!)

Erect or ascending perennial herb, 20.0–25.0 cm. tall; *stems* subterete, discolored with glabrous purple sides, pilose in the angles, essentially glabrous elsewhere, internodes 2.5–10.0 cm. long; *leaves* ovate-lanceolate, 8.0–8.5 cm. long, 1.0–1.8 cm. wide, sparingly sub-appressed hirsute on both sides, longer hairs on the margins and the chief veins beneath, bases of the hairs sometimes glandular, blades irregularly dentate, teeth small, about equally green below and above, firm; *petioles* slender, 1.0–2.0 cm. long, densely pubescent on upper surface; *peduncles* solitary, slender, 14.0–27.0 cm. long, densely pilose with spreading or erect grayish-white hairs, increasing in density above; *heads* 2.8–3.0 cm. wide, 1.0–1.5 cm. high; involucre 2-seriate, the outer phyllaries unequal, oblong or oblong-lanceolate, acute, pilose, the inner phyllaries shorter, oblong, acute or acuminate, glabrous or slightly puberulous; *rays* 14–18, 6.0–8.0 mm. wide, 1.9–2.3 cm. long, bright yellow, oblong, bluntly 2–3 cleft, puberulous at the base, glabrous on back side; *disk corollas* yellowish-orange, 4.0–5.0 mm. long, glabrous; *pales* oblong-lanceolate, obtuse, glabrous, narrowly keeled, thickened toward the apex, brownish-yellow above, 3.5–4.0 mm. long; *achenes* epappose, *ray achenes* obovoid, triangular, faintly nerved, sparingly pubescent on the angles, 3.0–3.2 mm. long; *disk achenes* oblong, abruptly quadrangular, faintly nerved on the faces, dull glabrous, crenulate near the apex, 2.5–3.0 mm. long.

Type locality.—Colombia: Dept. of Santander: Eastern Cordillera, vicinity of Vetas, alt. 3100–3250 meters.

Distribution.—Known only from type locality.

The lanceolate leaves, discolorous, purple, and glabrous stems, large heads on densely pubescent peduncles are the outstanding characters of this species. Herbarium material is limited and has only been collected from the type locality.

13. *Heliopsis helianthoides* (L.) Sweet, Hort. Brit. 487, 1826.

Erect perennial herb, 1.0–1.5 m. tall, branched or unbranched, *stems* terete, smooth (ridged when dry), glabrous or pubescent, 3.5–5.0 mm. thick; *leaves* lanceolate, ovate-lanceolate or deltoid-ovate, 7.0–12.0 cm. long, 3.0–6.0 cm. wide, glabrous to scabrous, *petioles* 0.2–3.5 cm. long, margin coarse, irregularly dentate; *peduncles* 9.0–25.0 cm. long, glabrous to scabrous; *heads* 0.9–2.5 cm. wide; *involucre* 2–3 seriate, phyllaries lanceolate to ovate, acute to obtuse, outer phyllaries usually foliar, yellow to orange-yellow above, 1.2–3.5 cm. long, 0.5–1.3 cm. wide, linear to ovate; *pales* 8.0–8.5 mm. long, 0.9–2.0 mm. wide, obtuse, membranaceous to slightly puberulous,



FIGURE 6. Distribution of *H. helianthoides* ssp. *helianthoides* (open circles); *H. helianthoides* ssp. *occidentalis* (solid circles); *H. helianthoides* ssp. *scabra* (x); *H. gracilis* (solid flags).

brownish-yellow at apex; *disk corollas* brownish-yellow; *ray achenes* triangular, outer surface convex, 3.0–3.5 mm. long, epappose or pappus represented by 2–3 membranaceous teeth, *disk achenes* quadrangular at apex, rounded at base, 3.0–3.5 mm. long, otherwise as ray achenes.

From an examination of the literature and herbarium material, it is evident that there has been a great deal of confusion in regard to the taxonomic status of this species. It is interesting to note the remarks made by Torrey and Gray in "Flora of North America" (1843): "We have so many forms intermediate between *H. laevis*, *H. scabra* and the very slender variety *gracilis*, that we unite them without the slightest hesitation; although the extremes appear abundantly different."

Heliopsis helianthoides consists of three distinct taxa with well defined centers of distribution,

namely the Appalachian region, the Ozark region and upper Great Plains region (fig. 6). Intergradation of characters occurs over a broad zone of hundreds of miles where the ranges of the taxa overlap (Fisher, submitted for publication). The hybridization study has shown that there are no reproductive barriers between these three taxa, and since they are morphologically distinct within their own centers of distribution, it seems advisable to reduce *H. scabra* Dun. and *H. helianthoides* (L.) Sweet to subspecies. Since the taxon of the upper Great Plains region has never been described, a new subspecies, *H. helianthoides* ssp. *occidentalis* has been proposed.

Because of the intergradation of characters, especially between ssp. *helianthoides* and ssp. *occidentalis*, annotation of herbarium material is extremely difficult. Those plants which closely resemble ssp. *occidentalis*, but have some characteristics of ssp. *helianthoides*, have been annotated as *H. helianthoides* ssp. *occidentalis* cline ssp. *helianthoides*.

Key to Subspecies of Heliopsis helianthoides

- A. Leaves, peduncles and phyllaries glabrous to minutely pubescent, leaves ovate-lanceolate, 4.5–6.0 cm. wide, 8.0–12.0 cm. long, cuneate, heads 1.2–1.8 cm. wide, peduncles 5.5–8.0 cm. long. ssp. *helianthoides*
- A. Leaves, peduncles and phyllaries scabrous, leaves deltoid or narrowly ovate-lanceolate.
 - B. Leaves linear to ovate-lanceolate, 8.0–12.0 cm. long, 3.0–3.5 cm. wide, petioles 2.0–2.5 cm. long, head 1.2–1.4 cm. wide. ssp. *scabra*
 - B. Leaves deltoid, 7.0–10.0 cm. long, 2.5–4.0 cm. wide, petioles 1.5 cm. long to nearly sessile, head 1.5–2.5 cm. wide. ssp. *occidentalis*

13a. *Heliopsis helianthoides* (L.) Sweet ssp. *helianthoides* Fisher comb. nov.

Buphthalmum helianthoides L. Sp. Pl. 904, 1753. (T.: Linnean Herbarium).

Silphium helianthoides L. Sp. Pl. 920, 1753.

Silphium solidaginoides L. Sp. Pl. 907, 1753.

Heliopsis laevis Pers. Syn. 2: 473, 1807.

Helepta grandiflora Raf. Neogynt. 3, 1825.

Helepta angustifolia Raf. Neogynt. 3, 1825.

Helepta parvifolia Raf. Neogynt. 3, 1825.

Heliopsis scabra var. *minor* Farwell, Mich. Acad. Sci. 19: 250, 1917. (T.: Farwell 4330 MICH!)

Heliopsis scabra var. *intermedia* Farwell, Mich. Acad. Sci. Rep. 19: 249, 1918. (T.: Farwell 4349 MICH!)

Heliopsis helianthoides var. *scabra* (Dun) Fernald, Rhodora 44: 340, 1942.

Heliopsis helianthoides var. *solidaginoides* (L.) Fernald, Rhodora 39: 456, 1937.

Stems glabrous; leaves ovate-lanceolate to ovate-oblong, 8.0–12.0 cm. long, 4.0–6.0 cm. wide, lower surface glabrous to sparingly pubescent, petioles 2.5–3.5 cm. long, glabrous; peduncles 9.0–13.0 cm. long, glabrous or slightly pubescent above; heads 0.9–1.5 cm. wide; phyllaries glabrous to sparingly pubescent; rays 10–12 pale yellow below, golden yellow above, 3.0–3.5 cm. long, 0.6–1.0 cm. wide.

Type locality.—"In America spetentrionalis, habitat in Virginia, Pennsylvania and Carolina." Linnaeus, Sp. Pl. 904, 1753. (Linnean Herbarium).

Distribution.—Eastern United States west to Indiana, Illinois, Kentucky, southeast to south central Georgia (fig. 6).

E. E. Sherff of Field Museum, Chicago, has distributed photographs of the type to several major herbaria of this country. On some of the photographs he has noted that the writing is in Linnaeus' hand. There is no question that the type description was drawn from the glabrous, smooth-leaved taxon of the Appalachian region.

This subspecies is centered in the Appalachian mountain region where it is relatively homogeneous. In the western portion of its range, however, namely Michigan, Indiana, and Illinois, there is a great deal of character intergradation with ssp. *occidentalis*. As a result, a broad zone of intermediate plants occur where the subspecies ranges overlap.

13b. *Heliopsis helianthoides* (L.) Sweet ssp. *occidentalis* Fisher ssp. nov. (T.: O. A. Stevens s.n. F! 885323, isotype UC 588923!).

Herba 1.0–1.5 m. alta; folia ovato-deltoida, scabra, 2.0–4.0 cm. lata, 7.0–10.0 cm.

longa, petioli 0.2–1.5 cm. longi; pedunculati 12.0–25.0 cm. longi, sparse scabri; capitula 1.5–2.5 cm. lata.

Stems sparingly scabrous below to hispidulous scabrous above; *leaves* deltoid to deltoid-ovate, sparingly scabrous below, hispidulous scabrous above; *petioles* 0.2–1.5 cm. long, sparingly pubescent; *peduncles* 12.0–25.0 cm. long, sparingly pubescent below, densely scabrous above; *heads* 1.5–2.5 cm. wide, phyllaries scabrous; *rays* 12–15, pale yellow below, golden yellow above; 2.5–3.0 cm. long, 1.0–1.3 cm. wide.

Type locality.—North Dakota: Cass Co.: near Fargo in edge of thicket.

Distribution.—Southeastern Canada and northeastern United States west to Illinois, Wisconsin, Minnesota, the Dakotas and southern Saskatchewan south to Colorado and central New Mexico (fig. 6).

Much of the herbarium material of the Ozark region of Missouri, Arkansas, Oklahoma and Texas has been referred to as *H. gracilis* or *H. helianthoides*, while the taxon of the northern Great Plains has been referred to as *H. scabra*. *H. scabra* was described by Dunal from material collected along the Missouri River of the central and lower Great Plains Region of the United States. The exact type locality was not given but from the accompanying description it is obvious that he was not referring to the newly described taxon, *H. helianthoides* ssp. *occidentalis*, which is centered in the upper Great Plains region of Kansas, South and North Dakota, Nebraska and Minnesota. In addition to the scanty information in regard to the exact type locality, there is further evidence that the description was drawn from plants of Missouri or regions farther south because of reference made concerning the indument of the stems and the shape of the leaves. The original description states. "caulibus scabris, foliis scabris, ovate oblongo acuminate serratis . . ." Examination of several hundred herbarium specimens indicates that these characteristic features could not have been observed by Dunal from the taxon of the upper Great Plains region. This fact, unfortunately, was overlooked by taxonomists who have since published floras of the United States.

13c. *Heliopsis helianthoides* (L.) Sweet ssp. *scabra* (Dun.) Fisher comb. nov.

Heliopsis scabra Dun., Mem. Mus. Paris 5: 56, 1819.

Heliopsis laevis var. *minor* Hook., Comp. Bot. Mag. 1: 98, 1835.

Heliopsis laevis var. *scabra* (Dun.) Torrey and Gray, Fl. No. Amer. 2: 203, 1842.

Heliopsis minor (Hook.) Mohr, U. S. N. H. 6: 796, 1901.

Heliopsis helianthoides var. *scabra* (Dun.) Fernald, Gray's Manual of Botany, 8th ed: 1479, 1950.

Stems glabrous below, sparingly pubescent above; *leaves* lanceolate to ovate-lanceolate, sparingly pubescent below, scabrous above, *petioles* 2.0–2.5 cm. long, minutely pubescent; *peduncles* 11.0–17.0 cm. long, glabrous below, scabrous above; *heads* 1.2–1.4 cm. wide; phyllaries scabrous; *rays* 12–14, pale yellow below, orange-yellow above 1.2–1.4 cm. long, 0.5–0.6 cm. wide.

Type locality.—"Habitat Am. secus amnem Missouri." From the original description there is not doubt that the taxon referred to as *H. scabra* is typical of the plants of the lower Great Plains and Ozark region, the area from which the original plant must have been collected.

Distribution.—West central Illinois to southern Iowa, south to western Louisiana (fig. 6).

This subspecies is best separated from the others by the lanceolate or ovate-lanceolate leaves with long petioles. It can be further separated on the basis of pubescence, head size, and peduncle length.

ACKNOWLEDGMENTS

This paper represents a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Botany Department, Indiana University. The author wishes to express his appreciation to Dr. C. B. Heiser, Jr. for critical suggestions in directing this study.

LITERATURE CITED

- Cooper, C. C. and K. L. Mahony. 1945. Cytological observations of some Compositae. Amer. Jour. Bot. 22: 834-848. 1935.
- Fisher, T. R. 1954. The genus *Heliopsis* (Compositae). Ph. D. thesis (microfilm) University of Michigan Library.
- Fisher, T. R. Variation in *Heliopsis helianthoides* (L.) Sweet. (Submitted for publication).
- Gersdorff, W. A. and N. Mitlin. 1950. Insecticidal action of American species of *Heliopsis*. Jour. Econ. Ent. 43: 554.
- Grant, V. 1953. The role of hybridization in the evolution of the leafy-stemmed Gilias. Evol. 7: 51-64.
- Martin, J., F. Acree, Jr., and H. D. Haller. 1947. Correction on the source of "Affinin." Jour. Org. Chem. 12: 731-732.
-

Handbook of Histology. Karl A. Stiles. McGraw-Hill Book Co. Inc., New York. 4th ed. 1956. xiii+240 pp. \$3.00.

Of particular interest to the beginning student of animal histology but also of value to the more experienced worker is this handbook. It serves as a useful elbow guide for laboratory work in which histological examination and identification are made of the primary tissues and organs. In 25 short "chapters" the author gives suggestions for the proper interpretation of sections as viewed through the microscope, directions for identifying them, and then chapter by chapter gives an outline of the location, staining characteristics, and morphological details of cells composing respective tissues. Helpful tables and diagrams are included and there is a pronouncing glossary, as well as a list of selected references. This is an ideally helpful manual in which the material is skillfully arranged by a teacher who's experience has given him an insight into the students' problems of learning.

G. W. PRESCOTT

Butterflies of the American Tropics, Genus *Anaea*. William P. Comstock.

The American Museum of Natural History is publishing a new series of works of high quality, beautifully illustrated in color. The first one is "Butterflies of the American Tropics, Genus *Anaea*" by William P. Comstock, sponsored by the late Frank Johnson. Prepublication price will be \$20.00 per copy; after publication \$25.00. Those interested may contact The American Museum of Natural History, Central Park West at 79th St., New York 24, N. Y.

J. N. KNULL

A CHECK LIST OF THE BIRDS OF OHIO

With the Migration Dates for the Birds of Central Ohio

By DONALD J. BORROR

Department of Zoology and Entomology, The Ohio State University

"The field identification of birds is greatly facilitated if the observer knows what birds are apt to occur at any given time and place."

More than 350 species listed.

Residential Status (migratory, non-migratory, transient, summer resident, summer visitor, winter resident or visitor).

Numerical Status, (abundant, common, fairly common, uncommon, rare, very rare, casual).

Arrival (earliest date, average date.)

Departure (average date, latest date).

Bibliography of 167 references.

ORDER YOUR COPY NOW—Send \$1.00 each (postpaid)
(Special Discounts on lots of 10 or more mailed to same address)

THE OHIO JOURNAL OF SCIENCE

THE OHIO STATE UNIVERSITY, COLUMBUS 10, OHIO

"Life-Like" VINYL PLASTIC MODELS



Please write for FREE Biology Catalog: OJS-B57



A.J. NYSTROM & Co. 3333 N. Elston Ave.
Chicago 18, Illinois